



MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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DEDICATION TO MICHAEL G. SIMPSON



The California Botanical Society is pleased to dedicate Volume 63 to Dr. Michael (Mike) G. Simpson Professor of Biology at San Diego State University in recognition of his contributions to the field of plant systematics and for his three decades of inspiring teaching and mentorship.

Mike received his bachelor's degree in botany from the University of Florida, Gainesville, in 1976. He earned his master's degree in botany from the University of North Carolina, Chapel Hill in 1979, and then completed his Ph.D. in botany with a minor in zoology at Duke University only four years later. For his graduate research, he focused on the systematics of the Haemodioraceae, or bloodwort family, a group of monocots distributed primarily in Australia and containing familiar ornamental plants such as kangaroo paws (*Anigozanthos* Labill.). With an uncanny eye for focusing on small details that would become a hallmark of his career, Mike developed new taxonomic characters from his study of pollen ultrastructure, embryo development, and floral anatomy to improve a then variable classification in the family.

Mike's current professional interests include plant systematics, biogeography, floristics, palynology, and plant embryology. He has broad taxonomic expertise in the Boraginaceae of the Americas, a focus that has led to a general interest in the American Amphitropical

Disjunction biogeographic pattern in plants. Mike has been actively publishing on these topics, but perhaps his most impressive achievement to date is the sole-author publication of his textbook, *Plant Systematics*, winner of the New York Botanical Garden's Henry Allan Gleason Award. Now in its second edition, this textbook has been widely adopted for its clear style, diversity of topics covered, and extensive illustrations and photographs - nearly all of which were made or taken by Mike over the years. In this age of increasing individual specialization and 10+ author papers, it is rare and refreshing to find someone with Mike's unique breadth and depth of knowledge.

Research aside, perhaps Mike's greatest gifts are in the realm of teaching and mentorship. Mike has masterfully lead countless students through challenging courses such as Plant Systematics, Taxonomy of California Plants, Economic Botany, and Principles of Organismal Biology. For his botany courses, Mike uses a number of innovative strategies to help students tame the voluminous information presented, such as an interactive, Socratic approach to teaching that develops student knowledge through regular student-teacher dialog, and early adoption of web-based course content. Mike's approach to teaching and passion for the subject matter help nearly all students to achieve high marks in his courses despite their level of difficulty.

Most importantly, students learn to appreciate the beauty and diversity of our green world; many are the botanists of California who can trace their love of plants directly to one of Mike's courses!

In the lab, Mike has personally mentored over 50 undergraduate and 14 graduate students. With an approach in the lab that mirrors that of the classroom, Mike is often highly involved with his mentees' research. Although constantly embracing new data types and analytical methods, Mike encourages students to stay grounded in observing plants in the field and herbarium; all of his students' projects involve some type of morphological analysis. Although students are free to pursue projects of their own choosing, Mike often recommends study of "difficult" taxonomic groups that require careful morphological and phylogenetic study, such as *Cryptantha* Lehm ex G. Don s.l. (Boraginaceae), *Pogogyne* Benth. (Lamiaceae), and *Calyptridium* Nutt. (Montiaceae). Even in these challenging groups, Mike and his students regularly succeed in producing logical and highly intuitive research products - be they floristic treatments, phylogenetic studies, or classifications - based on rigorous field, herbarium, and lab studies. In addition to professional preparation, students in Mike's lab will always be asked about their personal motivation to study plants in graduate school and beyond. Few labs have a mission statement, but the following was ours in the Simpson Lab and to this day it seems an excellent summary of the best reasons to study biology:

- To explore the beauty and grandeur of nature and to help preserve it;

- To engage in the spirit of scientific discovery;
- To experience and share the joy of learning.

Mike is as easy to admire personally as he is professionally. He is generous with his time, patient, even-keeled, and supportive. He has a true zest for life, and at any time his quest for life-long personal growth may manifest in an entirely new research direction, the steady attainment of a new language, or mastery of a new sport. He delights in the small details and has an infectious enthusiasm that brings others along for the ride. And despite the professional accolades and admirable personal qualities, Mike does it all without ego. He enjoys helping others to stand taller, and through his contributions many have done just that.

Since his retirement from San Diego State University in 2015, Mike has remained active in botanical research. With on-going affiliations at San Diego State, the San Diego Natural History Museum, and Rancho Santa Ana Botanic Garden, he will continue his important taxonomic work on the Boraginaceae. Given his growing interest in South American borages in particular, he plans to spend a portion of each of the coming years in Chile and Argentina, refining his Spanish and admiring all the countless, new "small details" that the plants there have to offer. On behalf of all who have benefited from your work, thank you Mike, but please don't spend too much time in South America - you are still needed here.

—C. MATT GUILLIAMS, Santa Barbara Botanic Garden, Santa Barbara, CA 93105. mguilliams@sbbg.org

NOTEWORTHY COLLECTION

CALIFORNIA

ELATINE AMERICANA (Pursh.) Arn. (ELATINACEAE). — Butte County, Gray Lodge Wildlife Area, west side of the dirt road, approximately 300 m NE of Parking Lot 10, 39.323000, –121.763083, small and medium-sized plants (≤ 5 cm in height), red, red-green, or green, prostrate or upright, emerged, growing on wet mud from ditch cleaning, uncommon, flowers and a few fruits present, 26 March 2015, L. Ahart 19966 (CONN); from the proximity of the previous collection, 39.328611, –121.830000, 10 April 2002, L. Ahart 9477 (CONN176566-00108517; CHSC82226) (previously misidentified as *Elatine ambigua* Wight).

Previous knowledge. *Elatine americana* was thought to grow naturally in California (e.g., Rydberg 1906; Jepson 1925, 1936; Abrams 1951). However, Mason (1957) determined all Californian populations of that taxon as *E. rubella* Rydb. Tucker (1993) and Tucker and Grissom (2012) also excluded *E. americana* from the flora of California in the first (TJM1) and second editions of the Jepson Manual (TJM2). Having subsessile flowers (lead 2. in TJM1 and TJM2 keys), *E. americana* could be confused with *E. ambigua*. Also, by having seed surface pits that sometimes are as long as wide (lead 5' in TJM1 and TJM2 keys), *E. americana* could be confused with *E. rubella*. Due to the overlap in such morphological features, herbarium specimens involving these species often are misidentified. Although all other *Elatine* L. species previously reported for the flora of California were detected during field surveys conducted throughout California in 2013–2014, no populations of *E. americana* were encountered at that time. However, through molecular studies, we eventually verified the presence of *E. americana* in California (Butte Co.), based on analysis of the misidentified collection of *E. ambigua* (Ahart 9477) cited above. Subsequent herbarium searches also yielded a 1926 specimen identified as *E. americana* (F. W. Peirson s.n. [PASA430]), collected in Modoc Co. However, that specimen is not *Elatine* but appears to be *Callitriche* L. on morphological grounds.

Significance. This report confirms the presence of *E. americana* within the flora of California, which currently represents the most westward location of this endemic species in North America. *Elatine americana* also occurs in Arizona (the sites nearest to the California occurrences), Connecticut, Delaware, Georgia, Illinois, Kansas, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana,

New Hampshire, New Jersey, New York, North Carolina, Oklahoma, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Vermont, and Virginia (herbarium records; USDA, NRCS 2015). *Elatine americana* is listed as endangered in Massachusetts, New York, and Pennsylvania; it is considered a plant of special concern in Rhode Island (USDA, NRCS 2015).

It is unclear whether the Californian populations of this species are native or naturalized occurrences. However, reports of this species in older literature (e.g., Rydberg 1906; Jepson 1925, 1936; Abrams 1951) indicate that *E. americana* might be native to California. Our preliminary molecular data (unpublished) indicate that *E. americana* is a hybrid species involving the native *E. rubella* and the nonnative *E. ambigua*. California is the only geographic area where the distributions of *E. ambigua* and *E. rubella* overlap. Also, the morphological intermediacy of *E. americana* relative to these two potential parental species (see *Previous knowledge*) strengthens the possibility of its hybrid origin. To evaluate this hypothesis, we recommend a thorough reexamination of *Elatine* populations in California and neighboring states, using molecular markers such as *matK*, nrITS, and *rbcL*, which have proven useful in our systematic studies of this genus.

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NOTEWORTHY COLLECTION

NEW MEXICO

CYPERUS GLOMERATUS L. (CYPERACEAE).
— Bernalillo County, City of Albuquerque, Rio Grande river terrace, numerous individuals, Albuquerque Overbank Project Site, 35.04314°N, 106.667542°W (WGS84), 1506 m, 30 September 2003, *Y. Chauvin 03AP001-G6* (UNM 113614); 34.975173°N, 106.689314°W (WGS84), 1504 m, 17 September 2004, *J. Cartron s.n.* (UNM106137); 35.135345°N, 106.691267°W (WGS84), 1520 m, 25 August 2010, *J. McGrath 1009* (UNM130756); 35.135345°N, 106.691267°W (WGS84), 1520 m, 30 September 2010, *J. McGrath 1019* (UNM130759); Harrison Site, 35.016233°N, 106.672762°W (WGS84), 1503 m, 12 September 2012, *P. Tonne 463, with E. Detweiler-Robinson & K. Robinson* (EIU, UNM); 35.016233°N, 106.672762°W (WGS84), 1503 m, 12 September 2012, *P. Tonne 465, with E. Detweiler-Robinson & K. Robinson* (EIU, UNM); State Land Office Site, 34.97091°N, 106.6861°W (WGS84), 1506 m, 13 September 2014, *P. Tonne 527, with A. Fretz and M. Bacigalupa* (AZ, ASU, BRIT, CO, K, MO, NMC, NY, TEX, UC, UNM, US);. Valencia County, City of Belen, Rio Grande river Site, 34.97091°N, 106.6861N, 106.742543°W (WGS84), 1466 m, 2 October 2008, *E. Milford 08MC001-G8* (UNM 128309); 34.638017°N, 106.742543°W (WGS84), 1466 m, 11 September 2009, *P. Tonne s.n.* (UNM).

Previous knowledge. *Cyperus glomeratus* is widespread in Asia and Europe (Dai et al. 2010), though its historic distribution appears to be poorly documented (Kavak 2014). It is listed as a non-native component of the Italian Flora (Celesti-Grappow et al. 2009).

Significance. This is the first report for the New World. How this species made its way to North America is a mystery. *Cyperus glomeratus* has been observed in mechanically created and established wetlands in the middle Rio Grande of New Mexico. It is most abundant on river margins and in sandy areas subject to overbank flooding.

It first came to our attention in 2003, when it was collected along the Rio Grande River in New Mexico, growing in a mechanically altered riparian site. The U.S. Bureau of Reclamation (BOR) impacted this site by lowering the riverbank of the Rio Grande in order to allow overbank flooding as part of the Albuquerque Overbank Project (Muldivin 2015). It appeared in two other BOR river restoration sites, the Crawford site in Belen, and the Harrison Middle

School site in Albuquerque. Most recently, this species rapidly colonized a newly created New Mexico State Land Office (SLO) excavated wetland in the south valley of Albuquerque. All of the BOR sites have a connection to the river, but the SLO site has no connectivity to existing channels. *Cyperus glomeratus* propagules may have been in the seed mix for the site, brought in on the heavy equipment, or introduced by an animal vector.

In two of the areas (Crawford and Harrison) where it was documented in habitat altered to allow overbank flooding, it was present in high abundance each fall for the first two years after the wetland was created but then disappeared, possibly due to a change in inundation of the area. We have seen it rapidly colonize three areas (Crawford, Harrison, and SLO) from seed, but its persistence within created and established wetlands warrants further investigation. It disappeared at the Crawford and Harrison sites. At the Crawford site it reappeared in very low abundance after 8 years of absence. At the Harrison site it has not been encountered in the past three years of surveys.

Cyperus glomeratus has not yet been documented outside of New Mexico, but it may already be spreading in the U.S. and Mexico. The Rio Grande connects with likely habitat in Texas and northern Mexico, downstream, and Colorado, upstream. Documentation of the range is needed, especially in these areas. In our opinion this is a weed that is here to stay; attempts to control it would likely be ineffective and more damaging than the presence of this plant in wetland habitat. Each plant has the potential to produce thousands of seeds from several inflorescences.

Cyperus glomeratus is the tallest *Cyperus* L. ([18] > 109 cm) with spikelets more densely arranged than any other *Cyperus* in New Mexico. We have three species of annual *Cyperus* with three stigmas and glomerulate heads (Tucker et al. 2003; Allred and Ivey 2012). *Cyperus glomeratus* has floral scales that are not keeled with obtuse apices; this separates it from *C. acuminatus* (2-keeled and acute, mucronate), *C. difformis* (not keeled, mucronate), and *C. squarrosus* (not keeled, cuspidate). Among native and naturalized *Cyperus* in The U.S. and Mexico, it would most likely be keyed to *C. ischnos* Schlecht. using Tucker (1994) or Tucker et al. (2002). *Cyperus ischnos*, however, is a perennial, montane species, with a whitish, capitate inflorescence.

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NOTEWORTHY COLLECTION

WYOMING

The following state records are from National Park Service units.

ALLIARIA PETIOLATA (M. Bieberstein) Cavara & Grande (BRASSICACEAE).—Crook County, Devils Tower National Monument at base of tower, T53N R65W Sec. 7, 1350 m, 5 September 2014, *M. Chapman and J. Balmagia s.n.* (RM, MORU). Growing in Ponderosa pine forest; subject of eradication effort.

Previous knowledge. Non-native perennial that is widespread in North America, including Nebraska and Utah (Al-Shehbaz 2010), Colorado (Weber and Wittmann 2012), Montana (Lesica 2012), Idaho (INVADERS Database 2015), and South Dakota (Black Hills State University Herbarium Database 2015).

Significance. First record for Wyoming, a range extension of about 70 km from Lawrence County, South Dakota.

CONYZA RAMOSISSIMA Cronquist (ASTERACEAE).—Crook County, Devils Tower National Monument, 0.4 miles southwest of entrance, T53N R65W Sec 18, 1183 m, 20 June 2012, *B. Heidel 3667* (RM, MORU). Growing in prairie dog town, with *Ambrosia psilostachya* DC., *Ceratocephala testiculata* (Crantz) Besser, *Conyza canadensis* (L.) Cronquist, *Verbena bracteata* Lag. & Rodr.

Previous knowledge. Native annual that is widespread in the Midwest and Great Plains, from North Dakota to Texas, east to Pennsylvania; sometimes a weed in lawns and open disturbed sites (Great Plains Flora Association 1986; Strother 2006).

Significance. First record for Wyoming (Heidel and Marriott 2014), a range extension of at least 50 km from Lawrence County, South Dakota.

PHYSARIA PACHYPHYLLA O’Kane & Grady (BRASSICACEAE).—Big Horn County, Big-horn Canyon National Recreation Area, Crooked Creek, T58N R95W Sec 35 NE of SE, 1152 m, 12 June 2001, *B. Heidel 1977* (RM), annotated by B. Grady. Growing on Chugwater outcrop with *Chrysothamnus nauseosus* (Pall. ex Pursh) Britton var. *graveolens* (Nutt.) H.M. Hall, *Wyethia scabra* Hook.

Previous knowledge. Native perennial, endemic to Pryor Mountain Desert of Montana near the Wyoming state line (Grady and O’Kane 2007; O’Kane 2010).

Significance. First record for Wyoming, a minor range extension and lower elevation limit at edge of Pryor Mountain Desert.

—BONNIE HEIDEL, Wyoming Natural Diversity Database, Dept. 3381, 1000 E., University Ave., Laramie, WY 82071-3381.

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THE CLASSIFICATION OF CALIFORNIA VISCACEAE: AN ALTERNATIVE PERSPECTIVE

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ABSTRACT

The classification of Viscaceae in the second edition of the Jepson Manual (TJM2) differs radically from that in the first edition of the Jepson Manual (TJM1). The number of species of *Arceuthobium* M. Bieb. was reduced from 12 in TJM1 to three in TJM2, and for *Phoradendron* Nutt. reduced from seven species to four. The TJM2 treatment is conservative in regards to these taxa, and disregards many morphological, phenological, and other physiological discontinuities (e.g., host preferences) among the Viscaceae of California that have been consistently reported in the scientific literature since the 1960s. The species accepted in TJM2 have widespread geographical distributions containing distinct lineages, some of which we consider different species, and other lineages that may be considered cryptic taxa. These taxa are distinct enough, based on differences in morphology, phenology, host specificity, and geographic isolation, to warrant classification as species or subspecies. The taxonomic recognition of these taxa is of critical importance to resource managers that are responsible for mitigating economic impacts of these parasitic plants, or documenting and protecting rare mistletoes. We present an alternative treatment for the Viscaceae, which recognizes both the cryptic and distinct mistletoes in California. We provide a brief history of the taxonomic classification of mistletoes in California and why we believe the treatment proposed herein is a far better representation of the mistletoe diversity in the state. Keys and descriptions are provided for the identification of mistletoes in the field that use both morphological characters and host-mistletoe relationships.

Key Words: *Arceuthobium*, hosts, mistletoes, *Phoradendron*, Pinaceae, taxonomy, *Viscum*.

Two native genera of Viscaceae, *Arceuthobium* M. Bieb. and *Phoradendron* Nutt. occur in California, as well as the introduced species *Viscum album* L. The classification of Viscaceae in the second edition of The Jepson Manual (TJM2) (Kuijt 2012) recognized four species and two subspecies in *Phoradendron* and three species in *Arceuthobium*, and the introduced species of *Viscum* L. In the first edition of The Jepson Manual (TJM1) (Hawksworth and Wiens 1993), seven species were recognized in *Phoradendron*, 12 species and two subspecies in *Arceuthobium*, and one species in *Viscum*. A comparison of these treatments indicates that they represent diverse perspectives for classification of Viscaceae in California.

Mistletoes are parasitic angiosperms and some populations are associated with economic losses to commercially valuable timber species or nut crops. Forest managers and agricultural enterprises are interested in mistletoe classification, management, and potential negative impacts on tree growth and longevity or nut production. While several mistletoes are common and abundant on their host trees, others are rare species that are of special concern to conservationists.

Since the treatment of Viscaceae in TJM2 is the most recently published classification for this family in California, many scientists may be attempting to identify mistletoes using keys and descriptions that are inadequate for accurate identification of mistletoes occurring in the state. A short summary of the historical classification of Viscaceae in California, as well as an alternative treatment, which we consider an improved taxonomic system for mistletoes in the state, are provided. This treatment is practical and useful to botanists and other resource managers because it considers differences in ecology, morphology, phenology, host affinities, and geography among mistletoe populations in California.

PAST AND RECENT CLASSIFICATIONS OF CALIFORNIA VISCACEAE

Arceuthobium

Arceuthobium has long been considered a taxonomically difficult genus because of the morphological and phenological similarities among taxa (Gill 1935; Kuijt 1955; Hawksworth and Wiens 1972, 1996; Hawksworth et al. 2002).

Morphological reduction and similarity have contributed to problems identifying *Arceuthobium* taxa in the field and major differences in taxonomic treatments. However, because many of the dwarf mistletoes we recognize as species and subspecies are host specific, knowing the geographic location and correct host identification, allows taxa of *Arceuthobium* to be easily determined for most populations in California (see below, Identification of Viscaceae in California: Field Key to *Arceuthobium* species and Appendix 1; the key and Appendix 1 are primarily for field use and will not work well for herbarium collections, particularly if the location and/or host are not indicated on labels).

Engelmann, considered the “father” of *Arceuthobium* classification in North America, described most species of *Arceuthobium* that are known from the United States (Engelmann 1880). The validity of Engelmann’s species has been justified on the basis of discontinuities in geography (ecosystem affinity), ecophysiology (host preference), morphometrics, and qualitative morphology. Where some of the species recognized by Engelmann co-occur, they flower at different seasons of the year and thus are also reproductively isolated. The recent classification of the family in TJM2 (Kuijt 2012) placed into synonymy about half of the taxa described by Engelmann (1880).

The first monographic treatment of *Arceuthobium* for the United States recognized three species for California: *A. americanum* Engelm., *A. douglasii* Engelm., and *A. campylopodum* Engelm. (Gill 1935). Gill (1935) also treated eight taxa as “host forms” of *A. campylopodum*, including seven from California that were recognized by Engelmann (1880). Gill’s host-form system classified all dwarf mistletoes parasitizing a true fir (*Abies* Mill.) as *A. campylopodum* Engelm. forma *abietinum* (Engelm.) Gill, even if the dwarf mistletoe also parasitized hemlock (*Tsuga* [Endl.] Carrière) in the same locality. Gill’s treatment required that the mistletoe on hemlock be classified as *A. campylopodum* Engelm. forma *tsugensis* (Rosendahl) Gill, even though the mistletoe on the true fir and the mistletoe on the hemlock were morphologically identical. Gill’s host-form system lacked the recognition that a dwarf mistletoe could cross-infect more than one host species at the same location, which resulted in assigning different names for the same dwarf mistletoe based on each host relationship.

Hawksworth and Wiens (1972) published a monograph of *Arceuthobium*, which became the authoritative publication on the biology and taxonomy of the genus, where they recognized nine species and two special forms (formae speciales) of *A. abietinum* Engelm. ex Munz in California (Table 1). Hawksworth and Wiens

used morphology (shoot size and color, flower, and fruit characters), phenology (time of meiosis, flowering, and seed dispersal), palynology (pollen characters), chemical constituents (anthocyanins and flavonoids), cytology (chromosome characters), and host preferences and reactions (hosts and host response to infection) in support of their treatment.

Hawksworth and Wiens (1993) contributed the treatment *Arceuthobium* in TJM1, which recognized 14 taxa in California. This treatment was consistent with the later revised monograph of *Arceuthobium* (Hawksworth and Wiens 1996), which recognized 42 New and Old World species, four of which had two subspecies each, one race of *A. tsugense* (Rosendahl) G. N. Jones, and two formae speciales of *A. abietinum*. The revised monograph provided systematic and descriptive information for each taxon as well as detailed information on the biology, anatomy, physiology, ecological relationships, pathology, and management of dwarf mistletoes. This work also included several new species described for California, including *A. littorum* Hawksw., Wiens & Nickrent, *A. monticola* Hawksw., Wiens & Nickrent, and *A. siskiyouense* Hawksw., Wiens, & Nickrent (Hawksworth et al. 1992; Hawksworth and Wiens 1996) (Table 1).

Phoradendron

The first monograph of *Phoradendron* was published by Trelease (1916), wherein nine taxa were recognized in California. Wiens (1964) published a revision of the species of *Phoradendron* lacking cataphylls (acataphyllous), and recognized seven taxa in California. The latter work served as the backbone for the treatment of *Phoradendron* contributed by Hawksworth and Wiens (1993) in TJM1, that recognized *P. californicum* Nutt., *P. juniperinum* A. Gray, *P. densum* Trel., *P. libocedri* (Engelm.) Howell, *P. macrophyllum* (Engelm.) Cockerell, *P. pauciflorum* Torrey, and *P. villosum* (Nutt.) Nutt. Wiens and Hawksworth (2002) studied *Phoradendron* sect. *Pauciflorae* Engl., and recognized *P. densum*, *P. libocedri*, and *P. pauciflorum* as valid species commonly found in California. Thereafter, Kuijt (2003) published a monograph for *Phoradendron* recognizing four species in the state (*P. bolleanum* [Seem.] Eichler, *P. californicum*, *P. juniperinum*, and *P. serotinum* [Raf.] M. C. Johnston [with two subspecies]). The treatment for *Phoradendron* in TJM2 (Kuijt 2012) followed the 2003 classification, except that *P. serotinum* was treated as *P. leucarpum* (Raf.) Rev. & M. C. Johnston in the electronic on-line version (i.e., Jepson eFlora) based on the nomenclature proposed by Abbott and Thompson (2011).

TABLE 1. Comparison of the classifications for the California Viscaceae proposed here and by Kuijt (2012). Note that 12 taxa of *Arceuthobium* recognized here are synonymized under *A. campylopodum* by Kuijt. ¹Taxa described for California in Hawksworth and Wiens (1972) and recognized by Hawksworth and Wiens (1993, 1996). ²Taxon described for California in Mathiasen and Daugherty (2009a). ³Taxa described for California in Hawksworth et al. (1992) and recognized in Hawksworth and Wiens (1993, 1996). ⁴Recognized as a species in Wiens and Hawksworth (2002) and as *P. bolleanum* subsp. *densum* in Wiens (1964). ⁵Recognized as a species in Wiens and Hawksworth (2002) and as *P. juniperinum* subsp. *libocedri* in Wiens (1964). ⁶Recognized as *P. tomentosum* subsp. *macrophyllum* in Wiens (1964). ⁷Recognized as a species in Wiens and Hawksworth (2002) and as *P. bolleanum* subsp. *pauciflorum* in Wiens (1964).

	Mathiasen and Kenaley (2016)	Kuijt 2012 (TJM2)
<i>Arceuthobium</i>	<i>A. abietinum</i> formae speciales <i>concoloris</i> ¹	<i>A. campylopodum</i>
	<i>A. abietinum</i> formae speciales <i>magnificae</i> ¹	<i>A. campylopodum</i>
	<i>A. abietinum</i> subsp. <i>wiensi</i> ²	<i>A. campylopodum</i>
	<i>A. americanum</i> ¹	<i>A. americanum</i>
	<i>A. californicum</i> ¹	<i>A. campylopodum</i>
	<i>A. campylopodum</i> ¹	<i>A. campylopodum</i>
	<i>A. cyanocarpum</i> ¹	<i>A. campylopodum</i>
	<i>A. divaricatum</i> ¹	<i>A. campylopodum</i>
	<i>A. douglasii</i> ¹	<i>A. douglasii</i>
	<i>A. littorum</i> ³	<i>A. campylopodum</i>
	<i>A. monticola</i> ³	<i>A. campylopodum</i>
	<i>A. occidentale</i> ¹	<i>A. campylopodum</i>
	<i>A. siskiyouense</i> ³	<i>A. campylopodum</i>
	<i>A. tsugense</i> subsp. <i>tsugense</i> ¹	<i>A. campylopodum</i>
	<i>A. tsugense</i> subsp. <i>mertensianae</i> ³	<i>A. campylopodum</i>
<i>Phoradendron</i>	<i>P. californicum</i>	<i>P. californicum</i>
	<i>P. densum</i> ⁴	<i>P. bolleanum</i>
	<i>P. juniperinum</i>	<i>P. juniperinum</i>
	<i>P. libocedri</i> ⁵	<i>P. juniperinum</i>
	<i>P. macrophyllum</i> ⁶	<i>P. serotinum</i> subsp. <i>macrophyllum</i>
	<i>P. pauciflorum</i> ⁷	<i>P. bolleanum</i>
	<i>P. villosum</i>	<i>P. serotinum</i> subsp. <i>tomentosum</i>
<i>Viscum</i>	<i>V. album</i>	<i>V. album</i>

Viscum

The European mistletoe (*Viscum album*) was intentionally established on fruit trees by the horticulturist Luther Burbank in Sebastopol, California in the early 1900s for the commercial Christmas ornament industry (Scharpf and Hawksworth 1976; Hawksworth and Scharpf 1986). It is now common in the farmland and communities surrounding Sebastopol (Hawksworth et al. 1991). This is the only example of an introduced mistletoe in the United States, and included in both editions of the Jepson Manual (Hawksworth and Wiens 1993; Kuijt 2012).

PROBLEMS RELATED TO THE CLASSIFICATION OF CALIFORNIA VISCACEAE

The conservative interpretation of Viscaceae in TJM2 facilitates identification of the species recognized. However, it ignores cryptic and distinct taxa present in California, which results in an underrepresentation of the state's mistletoe biodiversity. Some mistletoe species circumscribed in TJM2 have extensive geographical distributions that transcend widely differing ecosystems and habitats. For example, the treatment of *Arceuthobium campylopodum* in TJM2 includes 11 taxa as synonyms (previously

recognized as separate taxa in TJM1), and infects Pinaceae from southeastern Alaska to northern Baja California, then eastward through the Intermountain and Rocky Mountain states, and southward to western Texas (Kuijt 2012). Only two other species are recognized in TJM2, *A. americanum* and *A. douglasii*, which infect *Pinus contorta* Loudon and *Pseudotsuga menziesii* (Mirbel) Franco, respectively. Remarkably, no *Arceuthobium* described since 1880 is accepted in the TJM2 treatment of Viscaceae, which is essentially the same classification found in the *Manual of the Flowering Plants of California* (Jepson 1925). In contrast, we recognize 12 species of *Arceuthobium* in California here: the three species recognized in TJM2 and nine species that were reduced to synonymy under *A. campylopodum* (Table 1).

A study utilizing sequences of the nuclear ribosomal DNA (nrDNA; internal transcribed spacer [ITS] region) and those of non-coding chloroplast DNA (cpDNA), *trnT-L-F* by Nickrent et al. (2004) was cited in TJM2 as supporting evidence for reclassifying all species in *Arceuthobium* ser. *Campylopoda* found in California to synonymy under *A. campylopodum*. Although Nickrent et al. (2004) maintained *A. divaricatum* Engelm. as distinct from *A. campylopodum*, it was merged under *A. campylopodum* in TJM2.

Arceuthobium divaricatum is morphologically, physiologically, and genetically distinct from *A. campylopodum* (Hawksworth and Wiens 1972, 1996; Nickrent et al. 2004; Reif et al. 2015). Additional molecular analyses using DNA markers with improved phylogenetic resolution and greater genomic coverage are needed in order to better assess genetic differences and phylogenetic relationships as well as population and species boundaries we recognize among *Arceuthobium* ser. *Campylopoda* in California. To date, only two studies have examined the phylogenetic relationships among some (Nickrent et al. 1994) or all *Arceuthobium* spp. (Nickrent et al. 2004) we recognize in California.

Although the ITS and cpDNA regions are utilized routinely for resolving plant taxonomic issues due to their easy amplification and the availability of universal primers for both gene regions (Zimmer and Wen 2013), their phylogenetic resolving power remains poor or weak among some closely-related plants, including *Arceuthobium* spp. (Nickrent et al. 1994, 2004; Baldwin et al. 1995; Taberlet et al. 2007; Starr et al. 2009; Shaw et al. 2014). Current evidence suggests that morphology and/or ecological differences between closely-related plants may have evolved faster than commonly examined, “rapidly” evolving gene regions, such as ITS (Baldwin 2000; Álvarez and Wendel 2003; Feliner and Rosselló 2007). Thus, morphological and, in the case of dwarf mistletoes, host affinities may provide better fine-scale characters for recognizing evolutionary lineages than DNA data. Given these considerations, Reif et al. (2015) utilized amplified fragment length polymorphisms (AFLPs) and multivariate analyses of morphological data to examine the population genetics among *A. cyanocarpum* (A. Nelson ex Rydberg) Coulter & Nelson and two species not present in California, *A. blumeri* A. Nelson and *A. apacheum* Hawksw. & Wiens. Using this integrated approach, Reif and colleagues demonstrated that these taxa are distinct and should be recognized at the specific rank. Future research using AFLPs or advanced genotyping methods (e.g., genotyping-by-sequencing, see Elshire et al. 2011) should be conducted to examine genetic differences between population boundaries of *A. campylopodum* and its California relatives in order to estimate accurately the level(s) of inter- and intraspecific genetic differentiation among them.

The same problems related to grouping morphologically and physiologically distinct dwarf mistletoes under one species are also apparent for *Phoradendron* in TJM2. For example, two leafy conifer-infecting species, *P. densum* and *P. pauciflorum*, which were recognized by Wiens and Hawksworth (2002), are synonymized with *P. bolleanum* in TJM2. The latter species was

described from the Sierra Madre Occidental of Mexico (Seeman 1856). Wiens and Hawksworth (2002) studied *P. bolleanum* as far south as the Sierra Madre del Sur in tropical Mexico, and conducted field studies of *P. densum* and *P. pauciflorum* throughout California. They concluded that the latter species can be differentiated from *P. bolleanum* using morphology, phenology, and host affinities in California. This is supported by Ashworth (2000a, b) who used ribosomal DNA sequences (ITS and domains D1 and D8 of the 26S rRNA gene) to investigate relationships among *Phoradendron* taxa and found that *P. densum* and *P. pauciflorum* each possess a unique indel that distinguished these two species from *P. bolleanum*. Therefore, we concur with Wiens and Hawksworth (2002) and treat *P. densum* and *P. pauciflorum* as separate species.

Additionally, in TJM2, *Phoradendron serotinum* (= *P. leucarpum*; Reveal and Johnston 1989, Abbot and Thompson 2011) is recognized as a species, comprised of two subspecies: *P. serotinum* subsp. *macrophyllum* (Engelm.) Kuijt and subsp. *tomentosum* (DC) Kuijt. These taxa are not only morphologically distinct, but are usually restricted to different hosts and flower at different seasons of the year (summer versus winter) and are thus reproductively isolated (Wiens 1964). Therefore, we consider *P. macrophyllum* (*P. serotinum* subsp. *macrophyllum* in TJM2) and *P. villosum* (*P. serotinum* subsp. *tomentosum* in TJM2) as distinct species from *P. serotinum*. This conclusion is partially supported by sequence data (Ashworth 2000a, b) where *P. macrophyllum* and *P. villosum* were well segregated from each other based on the ITS sequence and indel data, but *P. macrophyllum* was not segregated from *P. serotinum*. We also classify *P. libocedri* as distinct from *P. juniperinum* based on morphology and host specialization, but this is not supported by ribosomal DNA data (Ashworth 2000a, b). Similar to our suggestions for further study of *Arceuthobium*, we suggest that molecular work utilizing more variable loci with greater genomic coverage should be undertaken to investigate phylogenetic and taxonomic relationships among closely related species of *Phoradendron*.

Pre-zygotic isolating mechanisms separate the California species of *Phoradendron* and include spatial or geographic isolation (restriction to specific ecosystems), ecophysiological isolation through habitat specialization (host specificity), and reproductive isolation where the flowering times of co-occurring (sympatric) species are partitioned over different seasons of the year (Wiens 1962, 1964). Hybridization is rare, worldwide, in both Loranthaceae and Viscaceae (Hawksworth and Wiens 1996; Polhill and Wiens 1998). In California, only two instances of

TABLE 2. Morphological measurements for *Arceuthobium campylopodum* and *A. cyanocarpum*. Data are listed as mean, (SD), n. Means followed by different capital letters in the same row were significantly different using Welch's t tests and the nonparametric Steel-Dwass, multiple comparison post hoc test ($\alpha = 0.05$). Data for *A. campylopodum* taken from Mathiasen and Kenaley (2015a) and for *A. cyanocarpum* taken from Reif et al. (2015). Plant heights are in cm and all other measurements in mm.

Character	<i>Arceuthobium campylopodum</i>	<i>Arceuthobium cyanocarpum</i>	P
Plant Height			
Female	10.4 A (2.7) 600	3.6 B (1.9) 258	<0.0001
Male	9.7 A (3.0) 600	2.8 B (1.8) 273	<0.0001
Basal Diameter			
Female	3.4 A (0.7) 600	2.0 B (0.4) 258	<0.0001
Male	3.2 A (0.6) 600	1.8 B (0.4) 273	<0.0001
Length of Third Internode			
Female	13.0 A (3.1) 600	2.0 B (0.4) 258	<0.0001
Male	12.0 A (3.3) 600	5.2 B (1.6) 273	<0.0001
Width of Third Internode			
Female	2.5 A (0.4) 600	1.5 B (0.2) 258	<0.0001
Male	2.5 A (0.4) 600	1.5 B (0.2) 273	<0.0001
Staminate Spike Length	12.0 A (4.7) 760	5.8 B (1.8) 294	<0.0001
Staminate Spike Width	3.0 A (0.3) 760	2.5 B (0.8) 294	<0.0001
Flower Diameter			
3-merous	3.1 A (0.4) 400	2.6 B (0.3) 220	<0.0001
4-merous	4.2 A (0.5) 360	2.8 B (0.5) 172	<0.0001
Petal Length	1.6 A (0.2) 760	1.3 B (0.2) 393	<0.0001
Petal Width	1.4 A (0.2) 760	1.1 B (0.2) 393	<0.0001
Anther Diameter	0.6 A (0.1) 760	0.5 B (0.2) 393	<0.0001
Anther Distance from Tip	0.6 A (0.1) 760	0.5 B (0.1) 253	<0.0001
Fruit Length	5.4 A (0.5) 480	3.5 B (0.4) 218	<0.0001
Fruit Width	3.7 A (0.4) 480	2.4 B (0.3) 218	<0.0001
Seed Length	3.5 A (0.4) 480	1.9 B (0.2) 208	<0.0001
Seed Width	1.5 A (0.4) 480	1.1 B (0.1) 208	<0.0001
Principal Hosts in California	<i>Pinus ponderosa</i> , <i>P. jeffreyi</i>	<i>Pinus flexilis</i> , <i>P. albicaulis</i>	

natural hybridization are known, both between *Phoradendron densum* and *P. juniperinum* (Wiens 1961; Vasek 1966). However, species integrity is not compromised because the hybrids are sterile (Wiens and DeDecker 1972). Therefore, the apparent lack of hybridization or sterility when rare hybrids occur in *Phoradendron* lends further support to the integrity of the species we contend are morphologically, genetically, and physiologically distinct.

We realize that morphological reduction and similarities in the inflorescences and flowers of both *Phoradendron* and *Arceuthobium* makes the circumscription of taxa challenging. Because of these traits, the Viscaceae in California (and elsewhere) require detailed studies and observations in nature to fully understand and quantify differences in their morphology, phenology, geography, and host specificity. A study of herbarium specimens alone may not be adequate, particularly if the aim is to quantify accurately the minute characters and landscape-scale patterns that define cryptic plants such as some taxa of *Arceuthobium* and *Phoradendron*. For these reasons, the Viscaceae of California require field study to clearly understand their ecological and taxonomic relationships (Wiens 1964; Hawksworth et al. 1992; Hawksworth and Wiens 1996; Wiens and Hawksworth 2002; Mathiasen and Kenaley 2015a).

Even with careful study, the overlap of some gross morphological characters (e.g., plant height and leaf size) may impede easy identification of some species. In such cases, differences among variable quantitative characteristics may be resolved by univariate and/or multivariate statistics (Quinn and Keough 2002) resulting in the identification of characters to assist with identification (Mathiasen and Kenaley 2015a, b; Reif et al. 2015). For example, Table 2 compares the morphological characteristics of two very distinctive dwarf mistletoes that occur in California, *Arceuthobium campylopodum* and *A. cyanocarpum*. Each morphological character measured is significantly different between the two species, demonstrating clear morphological differences. Furthermore, their host affinities in California are also quite distinct (Table 2; Figs. 1 and 2): *A. campylopodum* is a principal parasite of *Pinus ponderosa* Lawson and *P. jeffreyi* Grev. & Balf., whereas *A. cyanocarpum* is a principal parasite of *P. flexilis* James and *P. albicaulis* Engelm. (Hawksworth and Wiens 1996). Therefore, placing *A. cyanocarpum* in synonymy under *A. campylopodum* as proposed in TJM2 is not warranted; these two taxa are among the

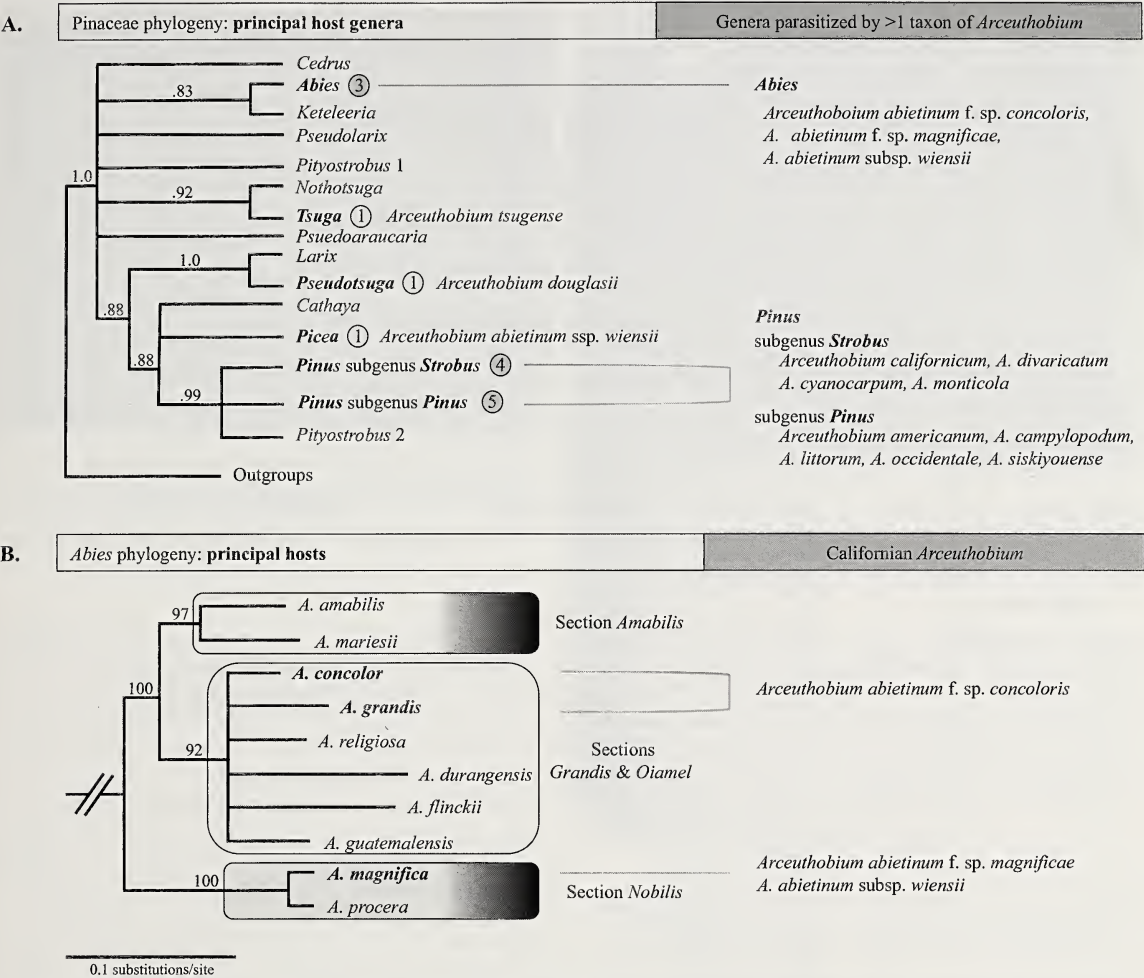


FIG. 1. Host-dwarf mistletoe relationships in California: principal host phylogenies and parasitizing taxa in the genus *Arceuthobium*. (A) Consensus tree comparing genera in the Pinaceae using combined, chloroplast DNA sequences (*matK* and *rbcL*) and morphological data (modification of Fig. 1F from Gernandt et al. 2008). The number of host-dwarf mistletoe combinations per genus/subgenus (circles) and corresponding *Arceuthobium* are provided. Principal host(s) of California *Arceuthobium* (bold) includes four separate genera (*Abies*, *Tsuga*, *Pseudotsuga*, and *Picea*) and two subgenera of *Pinus* (subg. *Pinus* and subg. *Strobus*). Numbers above branches represent Bayesian posterior probabilities after 5.0×10^7 generation (burn-in = 20%, total sample = 2.0×10^4 trees); branches with <0.80 support were collapsed. (B) Maximum likelihood analysis using the internal transcribed spacer (ITS) region of true firs (*Abies*) parasitized by taxa in *Arceuthobium* (modification of Fig. 3 from Xiang et al. 2009). Branch support was estimated using parsimony bootstrap analysis (1000 pseudo-replicates). Note that the principal host for the formae speciales of *A. abietinum* in California consists of two, phylogenetically distinct fir species, whereas, the principal host for *A. abietinum* ssp. *wiensii* includes *Abies magnifica* and *Picea breweriana* in Fig. 1A.

most morphologically and physiologically distinct species in ser. *Campylopoda* (Table 2; Figs. 3 and 4). Likewise, determining and recognizing taxa below the specific rank—the questions of subspecies—can also be facilitated by detailed morphologic analyses either alone or in combination with host affinity data.

Hawksworth and Wiens (1996) considered subspecies in *Arceuthobium* to be “geographically restricted populations of dwarf mistletoes that were distinguished by a few relatively small but consistent variations.” While morphological characters used to separate subspecies and species

of *Arceuthobium* often overlap, statistical analyses have demonstrated that some character means among subspecies are consistent and significantly different, regardless of the host (Wass and Mathiasen 2003; Mathiasen and Daugherty 2007; 2009a, Scott and Mathiasen 2009). Although Hawksworth and Wiens (1996) maintained that subspecies of *Arceuthobium* were geographically separate, field studies have now demonstrated that the geographic distributions of subspecies sometimes overlap. Thus, the key element of the subspecies concept in *Arceuthobium* is the relatively small but consistent

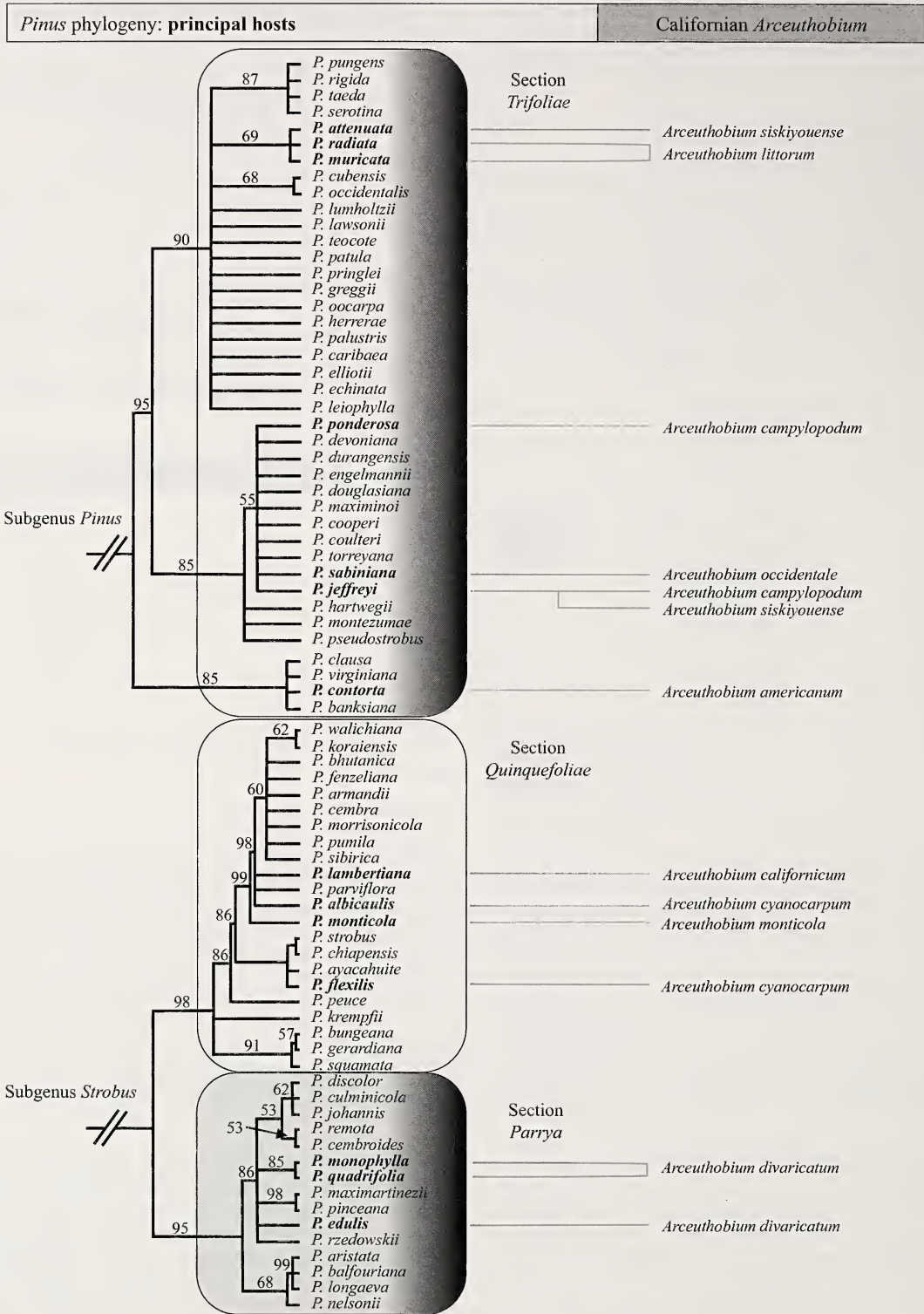


FIG. 2. Phylogeny of the genus *Pinus* (subg. *Pinus* and subg. *Strobus*) based on maximum parsimony analysis combining two chloroplast DNA gene regions (*matK* and *rbcL*; modification of Fig. 2 from Gernandt et al. 2005). Branch support was estimated via 500 bootstrap replicates. Note that, in California, 14 species of *Pinus* (bold) are recognized as principal hosts of a total of nine species of *Arceuthobium*. All host-dwarf mistletoe combinations are unique as no single-species of *Pinus* serves as a principal host to more than one species of *Arceuthobium*. Five species of *Arceuthobium* (*A. americanum*, *A. californicum*, *A. monticola*, *A. occidentale* and *A. siskiyouense*)



FIG. 3. Female plants of *Arceuthobium campylopodum* on *Pinus ponderosa* in late August with mature fruits. The largest plants are approximately 12 cm in length and the fruits are approximately 5 × 3 mm.



FIG. 4. Female plants of *Arceuthobium cyanocarpum* on *Pinus flexilis* in late August with mature fruits. The largest plants are approximately 4 cm in length and the fruits are approximately 3.5 × 2.5 mm.

differences among taxa. In addition, host affinities are critical in the classification of subspecies in *Arceuthobium* because differences in host preferences reflect corresponding and underlying genetic differentiation between taxa. Based on our analyses of morphological characters and knowledge of host affinities, we recognize three subspecies of *Arceuthobium* in California: two under *A. tsugense* (Hawksworth et al. 1992; Mathiasen and Daugherty 2007) and one under *A. abietinum* (Mathiasen and Daugherty 2009a). We have also continued the use of special forms under *Arceuthobium abietinum* proposed by Hawksworth and Wiens (1972, 1996), because we have observed that the populations of *A. abietinum* in the Cascade Ranges and Sierra Nevada parasitizing *Abies concolor* (Gordon & Glend.) Lindley do not infect *A. magnifica* Andr. Murray, and vice versa.

Field studies of species with extensive geographical distributions sometimes reveal the presence of evolutionarily autonomous cryptic taxa. The discovery and naming of cryptic lineages has been a common pathway for achieving greater understanding of species complexes and provides foundational knowledge for future experimental studies and surveys for plant biodiversity (Frankham et al. 2012). We, therefore, agree with Baldwin (2000) that cryptic taxa should be given taxonomic recognition as species, or at least subspecies, even though identification may be more difficult (see also the Philosophy

section of TJM2, pp. 1–2). As Baldwin (2000) emphasized, the cryptic differences between plant groups, such as characters associated with ecophysiology (e.g., host affinities for mistletoes, our addition), are more important to their survival and evolution than differences humans can observe visually. This concept definitely applies to the California Viscaceae.

THE IMPORTANCE OF HOST SPECIALIZATION IN CLASSIFYING THE CALIFORNIA VISCACEAE

Host-mistletoe relationships evident in California, and elsewhere, have evolved over thousands of years and remain one of the most important components in any taxonomic treatment of mistletoes, particularly *Arceuthobium*. Principal host-dwarf mistletoe combinations also provide insight into the evolution of the group. Yet the genetic and physiological mechanisms mediating host-specialization in mistletoes and the contribution of host preference to group speciation remain poorly understood. Host specialization is particularly important to forest resource managers and conservationists who are interested in either decreasing or increasing the abundance of these parasitic plants on the landscape. Any taxonomic treatment of this ecologically and economically important family that ignores host affinities of these relatively host-specific parasites is not representative of the genetic differences

← principally and separately parasitize only one species of *Pinus* in California. Three species of *Arceuthobium* (*A. campylopodum*, *A. cyanocarpum*, and *A. littorum*) are reported to parasitize principally and separately two closely related species of *Pinus*. Only *A. divaricatum* parasitizes more than two species of *Pinus* (pinyons) as principal hosts in California.

mistletoes have evolved over millennia (Hawskworth 1987, Hawskworth and Wiens 1996; Mathiasen 1996; Mathiasen and Kenaley 2015a, b).

The taxa we recognize herein are not only morphologically and/or phenologically distinguishable; their host affinities—particularly, principal host(s)—set them apart from each other (Figs. 1 and 2). For example, the treatment in TJM2 suggests that *Arceuthobium campylopodum* in California infects all Pinaceae genera except *Pseudotsuga* (Fig. 1A). However, years of field observations by botanists and foresters have demonstrated clearly that populations of *A. campylopodum* parasitizing *Pinus ponderosa* and *P. jeffreyi* in California do not parasitize *Abies concolor*, *A. grandis* (Douglas) Lindley (Fig. 1B), *Pinus monticola* Douglas, or *Pinus monophylla* Torrey & Frém. where these trees co-occur (Fig. 2; Hawskworth and Wiens 1996). However, secondary and occasional hosts of *A. campylopodum* include pines in section *Trifoliae* such as *Pinus attenuata* Lemmon and *P. coulteri* D. Don. *Arceuthobium campylopodum* also occasionally infects *P. contorta* and *P. sabiniana* Douglas (Hawskworth and Wiens 1996). While two additional taxa of *Arceuthobium* (*A. occidentale* and *A. siskiyouense*) also commonly infect *P. sabiniana* and *P. attenuata*, these dwarf mistletoes are differentiated from *A. campylopodum* by morphological differences and/or flowering period (Mathiasen and Kenaley 2015a). Furthermore, several dwarf mistletoes (not recognized as distinct species in TJM2) never infect the principal hosts of *A. campylopodum* (*P. ponderosa* and *P. jeffreyi*) in California including: *A. abietinum*, *A. californicum*, *A. cyanocarpum*, *A. divaricatum*, *A. monticola*, and probably *A. tsugense* (Hawskworth and Wiens 1996). Therefore, classifying all of these dwarf mistletoes under *A. campylopodum* completely ignores the host preferences and underlying genetic differences these species have evolved and negates the ability of foresters and conservationists to consider these important parasite-host relationships when managing dwarf mistletoes in California. Placing all of these species of *Arceuthobium* into synonymy with *A. campylopodum* also results in unrealistic distribution maps for dwarf mistletoes in California as illustrated by the CALFLORA map for *A. campylopodum* (<http://www.calflora.org/>) which actually represents the distribution of *A. campylopodum* and 10 other taxa we recognize as valid species or subspecies.

To further illustrate problems arising when species diversity is not recognized, consider the conservation of a cryptic species of dwarf mistletoe in the Klamath Ranges: *Arceuthobium abietinum* Engelm. ex Munz subsp. *wiensii* Mathiasen & C. Daugherty. If populations of

this dwarf mistletoe were classified as *A. campylopodum*, its host affinities would encompass most of the conifers found in the Klamath Ranges. However, this dwarf mistletoe only parasitizes *Picea breweriana* S. Watson, *Abies magnifica*, occasionally *A. concolor*, and rarely *Pinus monticola* in that region (Mathiasen and Daugherty 2009a). Therefore, in order to insure the survival of this host-specific parasitic plant, these hosts must be preserved where populations of this rare mistletoe exist. If this dwarf mistletoe's hosts were eliminated from the area by wildfire or logging activities and immune conifers were selected for recruitment or replanting following the disturbance(s), the dwarf mistletoe would probably not survive and could become extinct. Knowledge of this rare dwarf mistletoe's preferred habitat (host relationships) is critical to its preservation just as for any rare plant species. Failing to name and recognize the existence of this cryptic dwarf mistletoe lineage, as well as disregarding its ecological adaptations to certain habitats (hosts) would contribute to its potential loss. This is one example, or consequence, of how classifying the majority of the dwarf mistletoes in California as *A. campylopodum* could adversely affect their management and/or preservation.

There are additional examples of *Arceuthobium* populations in California with similar morphologies, yet they possess clear ecophysiological differences as demonstrated by their principal host preferences (Figs. 1B and 2). Probably the best example is illustrated by the populations of *Arceuthobium abietinum* parasitizing *Abies concolor* and *A. magnifica* in the Sierra Nevada. Both greenhouse studies and field observations have repeatedly supported the hypothesis that there are two morphologically similar, yet physiologically distinct populations: one that infects only *A. concolor* and not *A. magnifica*, and one that infects only *A. magnifica* and not *A. concolor* (Parmeter and Scharpf 1963; Scharpf and Parmeter 1967; Hawskworth and Wiens 1972, 1996). Because these populations are morphologically almost identical, while demonstrating a proven affinity for either *A. concolor* or *A. magnifica*, but not both, they were not given formal taxonomic status by Hawskworth and Wiens (1972, 1996) but were designated as special forms of *A. abietinum*. The morphological similarity of these populations has also been demonstrated by Mathiasen (2011). The circumscription of *A. abietinum* under *A. campylopodum* compromises the management of these populations for conservation purposes or for timber management decisions. As treated herein, *A. campylopodum* is a parasite of hard pines and not true firs and *A. abietinum* is primarily a parasite of true firs and causes considerable economic damage in forests of the Sierra Nevada (Scharpf and

Parmeter 1967; Hawksworth and Wiens 1996). This, in and of itself, is a valid reason for not applying the treatment for *Arceuthobium* in TJM2.

In *Phoradendron*, host affinities are also indicative of genetic differences among taxa. This is best typified by *P. libocedri* and *P. pauciflorum*. Each of these species parasitizes only one host; *Calocedrus decurrens* (Torrey) Florin and *Abies concolor*, respectively. These mistletoes are also morphologically distinct from other *Phoradendron* species (Wiens 1964; Wiens and Hawksworth 2002) although they are placed in synonymy under *P. juniperinum* and *P. bolleanum*, respectively, in TJM2.

Host preferences also delimit *P. juniperinum* and *P. densum* in California. As appropriately indicated by its specific epithet, *P. juniperinum* only parasitizes *Juniperus* throughout its geographic range. *Phoradendron densum*, however, occurs on *Juniperus* and several species of *Cupressus* in California and the Southwest (Wiens 1964; Wiens and Hawksworth 2002). The morphological differences between *P. juniperinum* and *P. densum* distinguish these taxa and host preferences and phenology further contribute to characterize *P. densum* as separate from *P. bolleanum* (Wiens 1964; Wiens and Hawksworth 2002), a species that was synonymized with *P. bolleanum* in TJM2. Finally, while both *P. villosum* and *P. macrophyllum* clearly have relatively large host ranges, *P. villosum* is primarily a parasite of *Quercus* in California and throughout its geographic distribution, while *P. macrophyllum* parasitizes a wide range of hardwood trees, but only rarely occurs on *Quercus* (Wiens 1964).

CONCLUSIONS

The California species of *Arceuthobium* constitute a particularly critical example of the value of giving taxonomic recognition to morphologically and physiologically differentiated populations because they are amongst the most economically and ecologically important plant pathogens of North American conifers (Hawksworth and Wiens 1996; Mathiasen 1996; Hawksworth et al. 2002; Mathiasen et al. 2008). If botanists, ecologists, conservationists, wildlife biologists, and especially foresters, are to make intelligent decisions regarding the preservation of mistletoe populations or sustainable harvesting of commercially valuable forest trees infected by mistletoes, they require the most current, specific, and definitive data available that are attendant to a species name. We submit that this treatment of California Viscaceae is of far greater practical value for resource managers and conservationists than that found in TJM2, and especially useful for identification of populations in the field.

In regions where the flora is relatively well known, the plant systematics community will once again have to confront the problem of how to define species and subspecies if cryptic plant lineages, as well as rare and endangered species, are to be protected and hence preserved. This is now a matter of critical environmental concern and natural scientists should embrace the classification of the California Viscaceae we propose as well as practical classifications for other plant groups as recommended by Baldwin (2000).

Lastly, we do not believe that the treatment of the California Viscaceae in TJM2, which is essentially a classification used before the year 1878, reflects, nor advances, the totality of knowledge presently available for the designation of species in this family. We, therefore, provide the following alternative treatment for the California Viscaceae which closely follows the treatment presented by Hawksworth and Wiens (1993), but improves upon their taxonomic keys, considers relevant literature published since then, and updates the classification of some taxa based on the discovery of an additional cryptic mistletoe in northern California.

IDENTIFICATION OF VISCACEAE IN CALIFORNIA

Mistletoe Family

Here we recognize Viscaceae (sensu Der and Nickrent 2008) as the family containing all of the mistletoes in California. Mistletoes are obligate parasitic plants of woody gymnosperms and angiosperms. They are dioecious or monoecious (dioecious in California), perennial, evergreen shrubs. Their stems are brittle with many branches and their leaves are simple, entire, opposite, four-ranked, with a blade or sometimes with scale-like leaves. Inflorescences are spikes or open cymes that are typically axillary, but sometimes terminal. The plants have bracts that are opposite, four-ranked, and scale-like, with each pair fused. Flowers are unisexual, radial, 2–5 mm wide and have perianth parts typically in one series. Staminate flowers have 3–4 (2–7) parts with anthers typically sessile, opposite, and borne on the perianth segments. Pistillate flowers have 2–4 perianth parts, an inferior ovary with one chamber, and an unbranched style with a relatively obscure stigma. The fruit is a berry containing mucilaginous viscin and typically has one seed, sometimes two. Viscaceous mistletoe seeds are dispersed by a variety of birds (*Phoradendron*) or explosively ejected from the fruit (*Arceuthobium*).

Because the following treatment for Viscaceae most resembles that found in TJM1 (Hawksworth and Wiens 1993), we have followed the treatments for the Cupressaceae (Bartel 1993) and Pinaceae (Griffin 1993) presented in TJM1.

FIELD KEY TO VISCACEAE GENERA IN CALIFORNIA

- 1. Stems generally <20 cm, may be angled, at least when young; leaves <1 mm, scale-like; fruits bicolored berries, explosive, somewhat compressed-spheric; pedicel recurved when mature; parasitic only on members of the Pinaceae in California *Arceuthobium*
- 1'. Stems >20 cm, rounded; leaves 5–80 mm, or scale-like and ≤1 mm; fruits one colored berries, not explosive, spheric; pedicel not recurved when mature; parasitic on angiosperms and gymnosperms
- 2. Perianth parts generally 3; inflorescence many flowered, open or interrupted spikes; flowers sunken into axis; berry diameter 3–6 mm; leaf (blade and pedicel) usually 5–50 mm long or scale-like, <1 mm; anthers 2 chambered; parasitic on angiosperms, occasionally on gymnosperms *Phoradendron*
- 2'. Perianth parts generally 4; inflorescence few-flowered, dense cymes; flowers not sunken into axis; berry diameter 6–10 mm; leaf (blade and pedicel) usually 50–70 mm long; anthers several chambered; parasitic on angiosperms *Viscum*

ARCEUTHOBIUM MARSCHALL VON BIEBERSTEIN

Dwarf mistletoe

These mistletoes are dioecious herbs or shrubs from 0.4–90 cm tall. Plants are glabrous and vary in color from green, greenish-yellow to yellow-brown, orange, purple, reddish, or black. Their leaves are reduced to minute, opposite, connate scales. Staminate flowers are generally decussate or rarely verticillate, and 2–5(-6) mm across, with a central nectary. Male flowers have (2-)3–4(-7) petals, each with a sessile, uniloculate, circular anther. Pollen grains are spherical with 6-alternating spiny and smooth sections. Pistillate flowers are epigynous with 1 style and 2 persistent petals that are adnate to the ovary, which has one chamber. Fruits are a bicolored, ovoid berry with one seed (rarely 2), enveloped in viscin, and recurved and explosive at maturity. Seeds lack true integuments and are usually 2–5(-6) mm long and 1–3(-4) mm wide, ovate-lanceolate with 1 (rarely 2) distal embryo.

Dwarf mistletoes are obligate parasites of trees in the Pinaceae in North America; elsewhere in the Old World there are species that parasitize trees in the Cupressaceae. Because they are widespread and common parasites, reduce the growth of their host trees, and are associated with premature mortality, they are considered to be

among the most serious and economically important forest pathogens in the United States. However, they are also recognized as important for many wildlife species because they provide food and habitat. Nearly all dwarf mistletoes induce the formation of dense masses of branches on infected trees called “witches’ brooms,” which not only aid in observing dwarf mistletoes, but serve as nesting, resting, and hiding sites for many species of birds and mammals.

Because species of *Arceuthobium* recognized here are relatively host specific, the following key facilitates identification of dwarf mistletoes by using known host preferences in California (Hawksworth and Wiens 1996). However, this then requires correct identification of the host(s) parasitized by the dwarf mistletoe under investigation.

More detailed botanical descriptions and nomenclature for each species or subspecies can be found in the reference(s) listed at the end of the Diagnostic Characters for each taxon. The full citations for the references are listed in the Literature Cited. Because upon drying, mistletoe plants often change color and the fruits can shrink significantly (25–30%), the following keys are primarily for field use and will not work as well for dried, herbarium collections.

FIELD KEY TO ARCEUTHOBIUM SPECIES IN CALIFORNIA

- 1. Parasites principally of *Pinus*
- 2. Parasites of *Pinus* subg. *Strobus* (D. Don) Lemmon with 1–5 needles per fascicle, one fibrovascular bundle per leaf (Haploxylon or soft pines)
- 3. Parasite of *Pinus monophylla* (1 needle per fascicle), *P. edulis* (2 needles per fascicle), and *P. quadrifolia* ([3]4[5] needles per fascicle) 8. *A. divaricatum*
- 3'. Parasites of *Pinus* subg. *Strobus* with 5 needles per fascicle (white pines) or *Picea breweriana* with 1 needle
- 4. Shoots usually less than 4 cm, yellow-green, densely clustered around the host branch, parasite of *Pinus albicaulis*, *P. flexilis*, *P. monticola*, and occasionally *P. balfouriana* 7. *A. cyanocarpum*
- 4'. Shoots usually more than 4 cm, dark brown or yellow-green, not densely clustered around the host branch, parasites of *Pinus lambertiana*, *Pinus monticola*, or *Picea breweriana*
- 5. Shoots dark brown, parasite of *Pinus monticola* and *Picea breweriana* in northwestern California 11. *A. monticola*
- 5'. Shoots yellow to green, parasite of *Pinus lambertiana* 5. *A. californicum*

- 2'. Parasites of *Pinus* subg. *Pinus* with 2-3 needles per fascicle, two fibrovascular bundles per leaf (Diploxylon or hard pines)
6. Plants branching in whorls; parasite principally of *Pinus contorta* 4. *A. americanum*
- 6'. Plants (at least some) branching flabellately; parasites principally of pines other than *Pinus contorta*
7. Plants green to dark green; not glaucous at base; basal diameter of female plants usually greater than 3.5 mm; staminate spike length usually greater than 15 mm; diameter of 3-merous and 4-merous flowers about 3.5 mm and 5 mm, respectively; 5-merous flowers common; anther diameter about 0.9 mm; parasite of *Pinus muricata* and *P. radiata* along the Pacific Coast 10. *A. littorum*
- 7'. Plants reddish-brown, yellow, yellow-brown, olive-green, or straw; occasionally glaucous at base; basal diameter of female plants usually less than 3.5 mm; staminate spike length usually less than 15 mm; diameter of 3-merous and 4-merous flowers about 3 mm and 4 mm, respectively; 5-merous flowers rare; anther diameter about 0.6 mm; parasitic on *Pinus attenuata*, *P. coulteri*, *P. jeffreyi*, *P. ponderosa*, or *P. sabiniana*
8. Plants dark brown or reddish brown, plants usually less than 10 cm; third internode widths usually less than 2 mm; staminate spike widths usually less than 2.5 mm; parasite of *Pinus attenuata* and *P. jeffreyi* in the Klamath Ranges 13. *A. siskiyouense*
- 8'. Plants yellow or brown or straw; plants usually greater than 10 cm; third internode widths usually greater than 2 mm; staminate spike widths usually greater than 2.5 mm; parasitic on *Pinus coulteri*, *P. jeffreyi*, *P. ponderosa*, or *P. sabiniana*
9. Plants primarily yellow or yellow-brown; third internode widths about 2.5 mm; fruits lightly glaucous; anthesis from late August to late September; parasite of *Pinus attenuata*, *P. coulteri*, *P. jeffreyi*, and *P. ponderosa* 6. *A. campylopodum*
- 9'. Plants yellow-brown or straw; third internode widths about 2.2 mm; fruits highly glaucous; anthesis from early October to December; parasitic primarily on *Pinus sabiniana* in the foothills surrounding the Great Central Valley, in the southern Sierra Nevada (Kern and Tulare counties), and on the north slope of the Transverse Ranges 12. *A. occidentale*
- 1'. Parasites principally of *Abies*, *Picea*, *Pseudotsuga*, or *Tsuga*
10. Parasites of *Pseudotsuga* or *Tsuga*
11. Shoots usually less than 3 cm long; flowering from April to May; parasite of *Pseudotsuga* 9. *A. douglasii*
- 11'. Shoots usually more than 3 cm long; flowering from August to September; parasites of *Tsuga*
12. Plants less than 5 cm; often green-brown; basal diameter of male and female plants 2 mm; mature fruits about 4 mm long and 3 mm wide; parasite of *Tsuga mertensiana* and occasionally *P. monticola* 15. *A. tsugense* subsp. *mertensianae*
- 12'. Plants usually more than 5 cm, green or yellow-green; basal diameter of male and female plants >2 mm; mature fruits about 4.5 mm long and 3 mm wide; parasite of *Tsuga heterophylla* near the coast of northern California 14. *A. tsugense* subsp. *tsugense*
- 10'. Parasites of *Abies* or *Picea*
13. Plants usually less than 10 cm, usually reddish brown; parasite of *Abies magnifica* and *Picea breweriana* in the Klamath Ranges, occasionally on *Abies concolor* 3. *A. abietinum* subsp. *wiensii*
- 13'. Plants usually more than 10 cm, yellow-green to green-brown; parasites of *Abies concolor*, *A. grandis*, or *A. magnifica*
14. Plants frequently green-brown; parasite of *Abies magnifica* in the Sierra Nevada 2. *A. abietinum* f. sp. *magnificae*
- 14'. Plants frequently yellow-green; parasite of *Abies concolor* and *A. grandis* 1. *A. abietinum* f. sp. *concoloris*

IDENTIFICATION OF *ARCEUTHOBIMUM* IN CALIFORNIA

The following section provides information needed to identify the taxa of *Arceuthobium* we classify as species, subspecies, or special forms in California. This section includes scientific names, most commonly infected hosts, distribution, a brief diagnostic description, and references to literature that provide more detailed descriptions for each taxon.

1. *Arceuthobium abietinum* Engelman ex Munz formae speciales *concoloris* Hawksworth & Wiens

White fir dwarf mistletoe

Hosts: The most commonly infected host of this dwarf mistletoe in California is *Abies concolor*. In far northern California, *A. grandis* is a principal host. In most instances when dwarf mistletoe is collected on *A. concolor* in California it should be identified as *A. abietinum* f. sp.

concoloris. This dwarf mistletoe will also infect *Pinus lambertiana* and infection appears to be more common than reported in the literature. However, when dwarf mistletoe is observed on *P. lambertiana* in California, it will usually be *Arceuthobium californicum* (see number 5 below).

Distribution: *Arceuthobium abietinum* f. sp. *concoloris* is common from the San Bernardino Mountains north through the Sierra Nevada and Cascade Ranges into Oregon and southern Washington. It is also common in the Klamath Ranges. It occurs in scattered populations in the North Coast Ranges.

In the Sierra Nevada there are populations of *A. abietinum* that only infect *Abies concolor* and populations that only infect *A. magnifica*, but plants of these populations are morphologically nearly identical. Because it has been demonstrated by many observations in mixed-conifer forests that the dwarf mistletoe on *A. concolor* will not infect *A. magnifica* and vice versa, these populations have been classified as special forms (*formae speciales*; f. sp.) This designation has no formal taxonomic status and should not be confused with subspecies (subsp.).

Diagnostic Characters: **Plants** 5–24 cm tall (mean 12), yellow or yellow-green, rarely green-brown. **Basal diameter** of dominant plants 2–6.2 mm (mean 3.6). **Staminate flowers** 3- or 4-merous, 3-merous flowers 2.1–3.5 mm in diameter (mean 2.7), 4-merous flowers 2.7–4.8 mm in diameter (mean 3.7). **Petals** 0.9–2 mm long (mean 1.4), 0.8–1.6 mm wide (mean 1.2), apex acute, same color as plants. **Anther** diameter 0.2–0.9 mm (mean 0.6). **Fruits** 3.3–6.1 mm long (mean 4.8) and 2.2–3.8 mm wide (mean 3.1), light green and lightly glaucous. **Seeds** 1.9–3.2 mm long (mean 2.5) and 0.8–1.6 mm wide (mean 1.2). **Anthesis** occurs from late June to mid October with peak flowering from mid July to late September. **Seed dispersal** starts in early September and ends in early November, but peak dispersal is from mid September to mid October. See Hawksworth and Wiens (1996, p. 179) and Mathiasen (2011) for additional descriptions of this species.

2. *Arceuthobium abietinum* Engelman ex Munz *formae speciales magnificae* Hawksworth & Wiens

Red fir dwarf mistletoe

Arceuthobium abietinum f. sp. *magnificae* is one of the principal disease agents of *Abies magnifica* in the Sierra Nevada. A canker-causing fungus, *Cytospora abietis* Sacc, often infects branches infected by this mistletoe. A symptom known as “flagging” is common on dwarf mistletoe-infected *A. magnifica* due to a combination of dwarf mistletoe and *Cytospora* killing the branch distal to the point of infection. As branches die,

needles turn red and then brown, and the infected branches can be easily observed. “Flagged” branches on *A. magnifica* make it relatively easy to observe dwarf mistletoe-infected trees in the Sierra Nevada.

Hosts: The only host of this dwarf mistletoe is *Abies magnifica*.

Distribution: *Arceuthobium abietinum* f. sp. *magnificae* occurs from near Mount Lassen (Shasta and Lassen Counties) to as far south as the southern Greenhorn Mountains (Kern County) east to the *A. magnifica* forests near Sherman Pass (Tulare County). Any dwarf mistletoe found on *A. magnifica* in this geographic area is *A. abietinum* f. sp. *magnificae*. This dwarf mistletoe is not known to cross infect any other hosts thus far. *Arceuthobium abietinum* subsp. *wiensii* can also be found on *Abies magnifica* in the Klamath Ranges (see number 3 below).

Diagnostic Characters: **Plants** 6–22 cm tall (mean 12), yellow, yellow-green, or green-brown. **Basal diameter** of dominant plants 2.1–7.6 mm (mean 3.6). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2.2–3.7 mm in diameter (mean 2.6), 4-merous flowers 2.6–5 mm in diameter (mean 3.6). **Petals** 0.9–2 mm long (mean 1.5), 0.8–1.7 mm wide (mean 1.2), apex acute, same color as plants. **Anther** diameter 0.3–0.9 mm (mean 0.6). **Fruits** 3.4–5.9 mm long (mean 4.7) and 2.2–3.9 mm wide (mean 3.1), light green and lightly glaucous. **Seeds** 1.8–3.3 mm long (mean 2.5) and 0.8–1.6 mm wide (mean 1.2). **Anthesis** peaks from early August to mid September. **Seed dispersal** peaks from early September to late October. See Hawksworth and Wiens (1996, p. 182) and Mathiasen (2011) for additional descriptions of this species.

3. *Arceuthobium abietinum* Engelman ex Munz subsp. *wiensii* Mathiasen & C. Daugherty

Wiens’ dwarf mistletoe

This dwarf mistletoe could have also been commonly referred to as Brewer spruce dwarf mistletoe because one of its principal hosts is *Picea breweriana*. However, it also severely parasitizes *Abies magnifica* and occasionally infects *A. concolor*, so its host range alone demonstrates that it is distinct from both *Arceuthobium abietinum* f. sp. *concoloris* and *A. abietinum* f. sp. *magnificae*. Given its limited geographic range and infection of *Picea breweriana* and *Abies magnifica*, this dwarf mistletoe is relatively easy to identify.

Hosts: *Arceuthobium abietinum* subsp. *wiensii* severely infects *Picea breweriana* and *Abies magnifica*. These hosts are about equally susceptible and in some populations of this dwarf mistletoe where *P. breweriana* is absent, *A. magnifica* is severely infected. *Arceuthobium abietinum* subsp. *wiensii*

will occasionally infect *Abies concolor*. In southern Oregon, it is sometimes observed on *Pinus monticola*, so it likely could be found infecting this host in northern California.

Distribution: *Arceuthobium abietinum* subsp. *wiensii* is common on *Abies magnifica* and occasionally infects *A. concolor* on Baldy Mountain (near Happy Camp), near Etna Summit, and on South Fork Mountain (near Mad River) in northern California. We presently know of only one location in California where this rare dwarf mistletoe occurs on *Picea breweriana*; near Baldy Mountain. Many severely infected *P. breweriana* are present on the east slopes of Baldy Mountain as well as many dead spruce killed by the mistletoe. This dwarf mistletoe also severely parasitizes *P. breweriana* at a few other locations in southern Oregon, so it is probable that it occurs on this host at other locations in northern California.

The geographic range of *A. abietinum* subsp. *wiensii* does not overlap with that of *A. abietinum* f. sp. *magnificae* and there is a distinct gap in the distribution of these dwarf mistletoes. We have been unable to locate any dwarf mistletoe infection of *Abies magnifica* near Mt. Shasta or west of there around Mt. Eddy, although this tree is common in those areas.

Diagnostic Characters: **Plants** 4–16 cm tall (mean 9), staminate plants green-brown, but may be red-brown, pistillate plants green-brown, but some red-brown or rarely yellow-brown. **Basal diameter** of dominant plants 1.8–5.8 mm (mean 3.2). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2–2.9 mm in diameter (mean 2.4), 4-merous flowers 2.6–3.8 mm in diameter (mean 3.2). **Petals** 0.8–2. mm long (mean 1.2), 0.7–1.4 mm wide (mean 1), apex acute, same color as plants. **Anther** diameter 0.4–0.7 mm (mean 0.5). **Fruits** 3.1–5.0 mm long (mean 4.2) and 2.2–3.5 mm wide (mean 3), light green and lightly glaucous. **Seeds** 1.9–2.9 mm long (mean 2.4) and 0.9–1.5 mm wide (mean 1.1). **Anthesis** from early July through late August with the peaks in late July to early August. **Seed dispersal** occurs from early September to mid October with peaks in late September to early October. See Mathiasen and Daugherty (2009a) for another description of this species.

4. *Arceuthobium americanum* Engelman

Lodgepole pine dwarf mistletoe

Arceuthobium americanum can easily be identified by its nearly exclusive parasitism of *Pinus contorta*, verticillate branching and attachment of fruits, slender plants, and spring flowering period (early April to early June).

Hosts: *Pinus contorta* subsp. *murrayana* (Grev. & Balf.) Critchf. is the principal host in California. This dwarf mistletoe occasionally parasitizes *P.*

ponderosa and *P. jeffreyi* when these pines are growing near infected *P. contorta* in California.

Distribution: This common dwarf mistletoe occurs from the San Bernardino Mountains north through the Sierra Nevada and Cascade Ranges to north-central and northeastern California. It is common throughout much of the geographic distribution of *P. contorta*.

Diagnostic Characters: **Plants** 5–9 cm tall (maximum 30), yellow or olive-green with verticillate branching. **Basal diameter** of dominant plants 1–3 mm (mean 1.5). **Staminate flowers** produced on pedicel-like segments, mostly 3-merous, but occasionally 4-merous, 3-merous flowers 2 mm in diameter. **Petals** approximately 1.1 mm long and 1 mm wide, same color as plants. Mean **anther** diameter 0.6 mm. **Fruits** verticillate, 3.5–4.5 mm long (mean 4) and 1.5–2.5 mm wide (mean 2). **Seeds** 2.4 × 1.1 mm. **Anthesis** is from late March to late June with peak flowering from early April to early June. **Seeds** are dispersed from late August to late September. See Hawksworth and Wiens (1996, p. 184) for a more detailed description of this species.

5. *Arceuthobium californicum* Hawksworth & Wiens

Sugar pine dwarf mistletoe

This dwarf mistletoe is only found in California and can be easily identified by its slender, green to yellowish-green plants, late spring to summer flowering period (mid June to late July), and by its exclusive parasitism of *Pinus lambertiana*. The only other dwarf mistletoe occasionally found on *P. lambertiana* in California, which could be confused with *Arceuthobium californicum*, is *A. abietinum* f. sp. *concoloris* (see number 1 above). Its thicker plants can distinguish the latter dwarf mistletoe and relatively poor shoot production on *P. lambertiana*. In addition, at locations where *A. abietinum* f. sp. *concoloris* occurs on *P. lambertiana*, infection of *Abies concolor* will be common and severe, while infection of the *P. lambertiana* in the stand will be obviously uncommon. In rare situations, both dwarf mistletoes may be present in an area, and in those cases, the two dwarf mistletoes maintain their preference for their principal hosts. Although both *A. cyanocarpum* and *A. campylopodum* have been reported infecting *P. lambertiana*, these crossover infections are extremely rare.

Hosts: The only confirmed host of this dwarf mistletoe is *P. lambertiana*. The report of *Arceuthobium californicum* on *Pinus monticola* is based on infection by *A. cyanocarpum* on this tree near Castle Lake southwest of Mount Shasta (Siskiyou County).

Distribution: *Arceuthobium californicum* occurs from the Klamath Ranges (near Dillon Moun-

tain, northwest of Orleans, Siskiyou County) south through the North Coast Ranges to near Clear Lake (Lake County). It also occurs in the southern Cascade Ranges from near Mount Lassen and then along the west side of the Sierra Nevada to as far south as the Kern River Drainage. It is also found in the San Bernardino, San Jacinto, and Cuyamaca Mountains of southern California.

Diagnostic Characters: **Plants** 6–15 cm tall (mean 10), greenish to bright yellow, turning brown at base of older shoots, flabellately branched. **Basal diameter** of dominant shoots 1.5–4.0 mm (mean 2.8). Flowers axillary. **Staminate spike** length 4.1–14.8 mm (mean 8.7), 1.1–2.1 mm wide (mean 1.8). **Staminate flowers** 3 or 4-merous, 3-merous flowers 1.9–3.4 mm in diameter (mean 2.6), 4-merous flowers 2.5–4.2 mm in diameter (mean 3.6). **Petals** 0.8–1.9 mm long (mean 1.2), 0.7–1.5 mm wide (mean 1.1), apex acute, same color as plants. **Anther** diameter 0.3–0.7 mm (mean 0.5). **Fruits** 4.3–6.0 mm long (mean 5.1) and 2.5–3.8 mm wide (mean 3.1), light green and lightly glaucous. **Seeds** 2.0–4.3 mm long (mean 2.7) and 0.8–1.6 mm wide (mean 1.2). **Anthesis** starts in mid June and ends in late August with peak flowering from late June to mid July. **Seed dispersal** occurs from mid September to mid October. See Hawksworth and Wiens (1996, p. 197) for another description of this species.

6. *Arceuthobium campylopodum* Engelmann

Western dwarf mistletoe

Its relatively thick, yellow, yellow-brown, or green shoots and parasitism of *Pinus ponderosa* and *P. jeffreyi* most easily identify *Arceuthobium campylopodum*. It typically induces the formation of large witches' brooms on infected trees, which often have swollen and resinous branches. It can be confused with *A. siskiyouense* in the Klamath Ranges where these mistletoes may co-occur and both infect *P. jeffreyi* and *P. attenuata*. However, *A. siskiyouense* is more slender and typically has reddish brown shoots (see number 13 below). *Arceuthobium campylopodum* is also common on *P. coulteri* and *P. attenuata*.

Arceuthobium campylopodum can also be confused with *A. occidentale* (see number 12 below). The primary distinction between *A. occidentale* and *A. campylopodum* is that the former species primarily parasitizes *Pinus sabiniana* in the foothills around the Great Central Valley and in the Coast Ranges. Female plants of *A. occidentale* also tend to be more tightly clumped together and the fruits are often very glaucous (bluish), so female plants are most useful for identifying these dwarf mistletoes from each other. Furthermore, *A. occidentale* consistently flowers later in the year (October to November) than *A. campylopodum* (August to September).

Hosts: *Pinus ponderosa* and *P. jeffreyi* are the principal hosts in California. *Arceuthobium campylopodum* also infects *P. attenuata*, *P. coulteri*, and *P. contorta* subsp. *murrayana*, but usually when these trees are associated with severely-infected *P. ponderosa* or *P. jeffreyi*. Throughout most of California the dwarf mistletoe likely found on *P. ponderosa*, *P. jeffreyi*, *P. coulteri*, or *P. attenuata* will be *A. campylopodum*. Only in the Klamath Ranges, where *A. siskiyouense* also occurs, will there be populations of two different dwarf mistletoes on *P. jeffreyi* and *P. attenuata*. These dwarf mistletoes can co-occur so they must be identified using the differences in their morphological characteristics in those situations. *Arceuthobium campylopodum* occasionally infects *P. sabiniana* on the western slopes of the Sierra Nevada, but again this usually occurs in locations where there is also severe infection on *P. ponderosa* or *P. jeffreyi*.

Distribution: *Arceuthobium campylopodum* is the most widely distributed dwarf mistletoe in California. It is common on *P. ponderosa* and *P. jeffreyi* from the Laguna Mountains (San Diego County) north through the Transverse Ranges, then through the Sierra Nevada and Cascade Ranges into the Modoc Plateau and Klamath Ranges. It is also common in the northern part—but not the southern part—of the Coast Ranges.

Diagnostic Characters: **Plants** 4–25 cm tall (mean 10), yellow, yellow-brown or olive-green. **Basal diameter** of dominant plants 1.7–6.9 mm (mean 3.3). **Staminate spike** length 3.7–41 mm (mean 12.7), 2.3–4.2 mm wide (mean 3). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2–4.5 mm in diameter (mean 3.1), 4-merous flowers 3–5.6 mm in diameter (mean 4.2). **Petals** 0.7–2.4 mm long (mean 1.6), 0.7–2.4 mm wide (mean 1.4), same color as plants. **Anther** diameter 0.4–1.2 mm (mean 0.6). **Fruits** 4–7.2 mm long (mean 5.4) and 2.6–5.6 mm wide (mean 3.7), light green and lightly glaucous. **Seeds** 2.3–4.7 mm long (mean 3.5) and 1–2 mm wide (mean 1.5). **Anthesis** occurs from early August to late September (early October in some years) with peak flowering from mid August to mid September. **Seed dispersal** primarily occurs between early September and early October. See Hawksworth and Wiens (1996, p. 199) and Mathiasen and Kenaley (2015a) for additional descriptions of this species.

7. *Arceuthobium cyanocarpum* (A. Nelson ex Rydberg) Coulter & Nelson Limber pine dwarf mistletoe

This dwarf mistletoe is identified by its parasitism of *Pinus flexilis* and *P. albicaulis*, small yellow-green plants that are densely clus-

tered around infected branches, and fruits that are usually highly glaucous (bluish).

Hosts: *Pinus flexilis* is the only host of this dwarf mistletoe on the east side of the Sierra Nevada and in southern California. On Mount Shasta, Black Butte, and near Mount Eddy it is found on *P. albicaulis*, but there it also commonly infects *Pinus monticola* and occasionally *P. balfouriana* Grev. & Balf. subsp. *balfouriana*. It has not been reported to infect the *P. balfouriana* subsp. *austrina* Mastrogioseppe & Mastrogioseppe populations in the southern Sierra Nevada. In Nevada and Utah, *P. longaeva* D. K. Bailey is also a common host, so this dwarf mistletoe may infect *P. longaeva* in California, but it has not yet been reported on this host.

Distribution: In California, *Arceuthobium cyanocarpum* only occurs on Mount Shasta, south and west of Mount Eddy, in a few scattered, isolated populations on the east side of the southern Sierra Nevada, and in a few locations in the San Bernardino and San Jacinto Mountains. However, it is widely distributed through the Rocky Mountains as far north as central Oregon and western Montana and east through southern Idaho, Nevada, Utah, and Colorado.

Diagnostic Characters: **Plants** 1–5 cm tall (mean 3), yellow, yellow-green, to rarely reddish. **Basal diameter** of dominant plants 1–3.5 mm (mean 1.9). **Staminate flowers** 3 or 4-merous, 3-merous flowers 1.9–3.5 mm in diameter (mean 2.6), 4-merous flowers 1.8–3.8 mm in diameter (mean 2.8). **Petals** 0.8–2 mm long (mean 1.3), 0.7–1.7 mm wide (mean 1.1), same color as plants. **Anther** diameter 0.2–0.7 mm (mean 0.5). **Fruits** 2.5–4.5 mm long (mean 3.5) and 1.7–3.2 mm wide (mean 2.4), light green and lightly to highly glaucous. **Seeds** 1.3–2.5 mm long (mean 1.9) and 0.8–1.5 mm wide (mean 1.1). **Anthesis** starts in early July and ends in mid September, but peak anthesis is between mid July and late August. **Seed dispersal** occurs from mid August to late September. See Hawksworth and Wiens (1996, p. 201) for another description of this species.

8. *Arceuthobium divaricatum* Engelm

Pinyon dwarf mistletoe

Arceuthobium divaricatum is easily identified because it is the only dwarf mistletoe found on pinyon pines in California and elsewhere in the United States.

Hosts: The most commonly infected pinyon pine in California is *Pinus monophylla*. *Arceuthobium divaricatum* has been reported to infect *P. quadrifolia* Parl. in the Laguna Mountains, California. It also infects *P. edulis* Engelm. in the New York and Clark Mountains, San Bernardino County. All other conifers are considered to

be immune to infection by this dwarf mistletoe. If the classification of several pinyon pine populations in southern California as *Pinus californiarum* D. K. Bailey subsp. *californiarum* and *P. californiarum* subsp. *fallax* (Little) D. K. Bailey is recognized, then note that these pinyon pines have also been reported as hosts of this dwarf mistletoe.

Distribution: *Arceuthobium divaricatum* occurs exclusively on pinyon pines and is locally abundant in scattered populations in the Transverse Ranges and several of the Desert Mountains of the Mojave Desert in San Bernardino and Inyo Counties. It also occurs in the eastern and southern Sierra Nevada, White Mountains, and Inyo Mountains.

Diagnostic Characters: **Plants** 5–30 cm tall (mean 11), green, brown-green, or brown. **Basal diameter** of dominant plants 1.3–5 mm (mean 2.5). **Staminate spike** length 3.2–31 mm (mean 9.1), 1.1–2.3 mm wide (mean 1.7). **Staminate flowers** 3-merous, occasionally 4-merous, 3-merous flowers 1.4–3.1 mm in diameter (mean 2.2). **Petals** 0.7–1.6 mm long (mean 1.1), 0.6–1.3 mm wide (mean 1.0), same color as plants. **Anther** diameter 0.3–0.6 (mean 0.4). **Fruits** green, lightly glaucous, 3.2–5.1 long (mean 4.3), 1.9–3.5 mm wide (mean 2.6). **Seeds** 1.6–3.1 mm long (mean 2.1), 0.8–1.3 mm wide (mean 1.1). **Anthesis** is from early August to early October, with peak flowering from late August to mid September. **Seed dispersal** is from early September to early November with a peak from mid September to mid October. See Hawksworth and Wiens (1996, p. 204) for another description of this species. This reference also discusses infection of *Pinus californiarum* by *Arceuthobium divaricatum* (pp. 204–205).

9. *Arceuthobium douglasii* Engelm

Douglas-fir dwarf mistletoe

Arceuthobium douglasii can easily be identified by its nearly exclusive parasitism of *Pseudotsuga menziesii*, small plants that often occur along infected branches after the second or third internode, its reddish to purple flowers, and its spring flowering period (April to early June). *Arceuthobium douglasii* induces the formation of large, round witches' brooms on infected trees. It is often difficult to find shoots on infected branches, particularly in dense forests where little light reaches the lower canopy.

Hosts: *Pseudotsuga menziesii* is the principal host throughout this mistletoe's geographic range.

Distribution: *Arceuthobium douglasii* has the greatest latitudinal range of any dwarf mistletoe, but in California it has only been found in the southern Cascade Ranges near Mount Lassen

and Mount Shasta, in the North Coast Ranges, and in the Klamath Ranges.

Diagnostic Characters: **Plants** 0.5–3 cm tall, mostly less than 2 cm, olive-green, secondary branches rare. **Basal diameter** of dominant plants 1–1.5 mm (mean 1). **Staminate flowers** usually axillary in pairs, occasionally borne on pedicel-like segments, mostly 3-merous, but rarely 2- or 4-merous, 3-merous flowers 2.3 mm in diameter. **Petals** approximately 1 mm long and 1 mm wide, apex rounded, inner surface of petals reddish to purple, lower surface same color as plants. Mean **anther** diameter 0.4 mm. **Fruits** olive green, 3.5–4.5 mm long (mean 4) and 1.5–2 mm wide (mean 1.7). **Seeds** 2.4×1.1 mm. **Anthesis** peaks from early April to late May, but can start as early as late March and extend to mid June. **Seed dispersal** occurs from late August to late September. See Hawksworth and Wiens (1996, p. 207) for a more detailed description of this species.

10. *Arceuthobium littorum* Hawksworth, Wiens, & Nickrent

Coastal dwarf mistletoe

Arceuthobium littorum is one of the least common dwarf mistletoes in the United States. It is only known from a few, isolated populations along the Pacific Coast of California from near Fort Bragg south to Cambria. This dwarf mistletoe was previously classified as *A. occidentale* (see number 12 below) and some investigators group this mistletoe under *A. campylopodum*; but, we consider it to be sufficiently differentiated by its plant color, male flower size, and its parasitism of *Pinus muricata* D. Don and *P. radiata* D. Don to be treated as a separate species. This dwarf mistletoe commonly forms male flowers with five petals, and rarely with six petals, which is not a characteristic of other dwarf mistletoes found in California.

Hosts: The principal hosts of this dwarf mistletoe are *Pinus muricata* and *P. radiata*. *Pinus muricata* is the principal host in the North Coast populations (north of San Francisco), while *P. radiata* is the host in the Central Coast populations. The rare *Pinus contorta* subsp. *bolanderi* (Parl.) Critchf. is also infected in areas where it is associated with severe infection on *P. muricata*.

Distribution: This dwarf mistletoe occurs in widely scattered populations along the North and Central Coasts from east of Fort Bragg (Mendocino County) to Cambria (San Luis Obispo County). Although only a few populations are known, it probably occurs in many additional areas, which have not been discovered yet; many of these areas are on private property near the coast. This is the dwarf mistletoe found on *Pinus radiata* in Carmel and Monterey.

Diagnostic Characters: **Plants** 5–19 cm tall (mean 10), dark green to green-brown. **Basal diameter** of dominant plants 2.6–7 mm (mean 3.7). **Staminate spike** length 6.1–55.9 mm (mean 20.6), 2.1–4.2 mm wide (mean 3.4). **Staminate flowers** 3-, 4-, or 5-merous, rarely 6-merous, 3-merous flowers 2.4–4.8 mm in diameter (mean 3.5), 4-merous flowers 3.4–6.9 mm in diameter (mean 5.2), 5-merous flowers 4.4–6.9 mm in diameter (mean 5.7). **Petals** 1.0–2.8 mm long (mean 1.9), 0.8–2.5 mm wide (mean 1.6), same color as plants. **Anther** diameter 0.4–1.5 mm (mean 0.9). **Fruits** 4–6.4 mm long (mean 5.4) and 2.9–4.4 mm wide (mean 3.6), dark green to reddish, not glaucous. **Seeds** 2.5–4.2 mm long (mean 3.4) and 1–1.6 mm wide (mean 1.3). **Anthesis** starts in late August, peaks in mid to late September, and ends by mid October. **Seed dispersal** starts in early September, peaks in late September and early October, and is completed by early November. However, there are reports of seed dispersal lasting into December. See Hawksworth et al. (1992), Hawksworth and Wiens (1996, p. 224), Mathiasen and Daugherty (2013), and Mathiasen and Kenaley (2015a) for additional descriptions of this species.

11. *Arceuthobium monticola* Hawksworth, Wiens, & Nickrent

Western white pine dwarf mistletoe

Arceuthobium monticola can be distinguished from *A. cyanocarpum* and *A. californicum* by its brown shoots and nearly exclusive parasitism of *Pinus monticola* in the Klamath Ranges.

Hosts: *Pinus monticola* is the principal host in California and *P. lambertiana* is rarely infected. However, in northern California this dwarf mistletoe severely parasitizes *Picea breweriana* as well, but only in a few locations (e.g., near Black Butte in western Siskiyou County).

Distribution: This dwarf mistletoe is rare in the Klamath Ranges of Del Norte and Siskiyou Counties. Although it also occurs in southern Oregon, the 2002 Biscuit Fire that burned approximately 500,000 acres on the Siskiyou National Forest destroyed several populations. Because of its rarity in northern California and southern Oregon, *A. monticola* should be considered for conservation status.

Diagnostic Characters: **Plants** 4–13 cm tall (mean 8), usually dark brown, but some staminate plants may be yellow. **Basal diameter** of dominant plants 2–3.8 mm (mean 2.9). **Staminate spike** length 5–14.2 mm (mean 8.6), 1.1–1.8 mm wide (mean 1.4). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2–3.1 mm in diameter (mean 2.5), 4-merous flowers 3–4.6 mm in diameter (mean 3.6). **Petals** 0.8–1.7 mm long (mean 1.3), 0.7–1.3 mm wide (mean 1.1), same color as plants. **Anther** diameter 0.4–0.8 mm (mean 0.5).

Fruits 4–5.6 mm long (mean 4.7) and 2.4–3.5 mm wide (mean 3), light green and lightly glaucous. **Seeds** 1.8–3.2 mm long (mean 2.5) and 0.9–1.4 mm wide (mean 1.2). **Anthesis** begins in mid-July, peaks in early- to mid-August, and continues into early-September. **Seed dispersal** starts in early September, peaks in late September, and is finished by late October. See Hawksworth et al. (1992), Hawksworth and Wiens (1996, p. 228), and Mathiasen and Daugherty (2009b) for additional descriptions of this species.

12. *Arceuthobium occidentale* Engelmänn

Gray pine dwarf mistletoe

Arceuthobium occidentale is similar in appearance to *A. campylopodum*. The primary distinction between *A. occidentale* and *A. campylopodum* is that the former species primarily parasitizes *Pinus sabiniana* in the foothills of the Sierra Nevada around the Great Central Valley and in the Coast Ranges of California. Female plants of *A. occidentale* also tend to be more tightly clumped together and the fruits are often very glaucous (bluish), so female plants are most useful for identifying these dwarf mistletoes from each other. Furthermore, *A. occidentale* consistently flowers in the fall (October to November) and *A. campylopodum* flowers in the late summer (August to September).

Hosts: *Pinus sabiniana* is the most commonly infected host, but both *P. coulteri* and *P. attenuata* are infected when growing near severely infected *P. sabiniana*. In addition, both *P. ponderosa* and *P. jeffreyi* are infected by *A. occidentale* in areas where these hosts are outside the range of their principal parasite, *A. campylopodum*, and they are growing among severely infected *P. sabiniana*. Furthermore, in some areas along the west side of the Sierra Nevada at the lower elevational range of *P. ponderosa*, *A. occidentale* will cause severe infection on *P. ponderosa* in the absence of *P. sabiniana*. This is one of the reasons some classifications group *A. occidentale* and *A. campylopodum* as the same species; their similar morphological characteristics are another reason. *Arceuthobium occidentale* has also been found infecting planted *P. radiata* growing near infected *P. sabiniana* on Mount Hamilton, California. But as far as is known, *A. occidentale* does not occur within the natural range of *P. radiata*. If dwarf mistletoe is observed on *P. radiata* it is most likely *A. littorum* (see number 10 above).

Distribution: This dwarf mistletoe is relatively common on *P. sabiniana* throughout the foothills surrounding the Great Central Valley and near the Kern River in the southern Sierra Nevada. It also is common in the Coast Ranges from near

Mount Pinos in Ventura County to as far north as eastern Mendocino County. Although it occurs near the Central Coast in Monterey and San Luis Obispo Counties, its range does not overlap with the *Pinus muricata* and *P. radiata* populations found there.

Diagnostic Characters: **Plants** 5–23 cm tall (mean 11), yellow, yellow-brown or dark brown, highly glaucous. **Basal diameter** of dominant plants 1.7–6.4 mm (mean 3.1). **Staminate spike** length 6.2–34 mm (mean 13.9), 2.2–3.9 mm wide (mean 2.9). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2.2–4.1 mm in diameter (mean 3), 4-merous flowers 3–6.2 mm in diameter (mean 4.1). **Petals** 1.1–2.5 mm long (mean 1.5), 0.7–2.2 mm wide (mean 1.3), same color as plants. **Anthor** diameter 0.4–1 mm (mean 0.6). **Fruits** 4–6.8 mm long (mean 5.2) and 2.4–4.7 mm wide (mean 3.3), light green and highly glaucous. **Seeds** 2.5–4.3 mm long (mean 3.5) and 1–1.7 mm wide (mean 1.3). **Anthesis** starts in early October, peaks in late October or early November, and finishes in mid December. **Seed dispersal** starts in early October, peaks in late October to early November, and ends in late December. See Hawksworth and Wiens (1996, p. 231), Mathiasen and Daugherty (2013), and Mathiasen and Kenaley (2015a) for additional descriptions of this species.

13. *Arceuthobium siskiyouense* Hawksworth, Wiens, & Nickrent

Knobcone pine dwarf mistletoe

Arceuthobium siskiyouense is most likely to be confused with *A. campylopodum*. However, *Arceuthobium siskiyouense* has more slender, reddish-brown plants than the thicker, yellow, yellow-brown or green plants of *A. campylopodum*. While this character is more difficult to observe, the width of the mature staminate spikes of *A. siskiyouense* are much more slender (mean 2 mm) than those of *A. campylopodum* (mean 3 mm).

Hosts: *Pinus attenuata* and *P. jeffreyi* are the principal hosts of *A. siskiyouense* in far northern California and *P. contorta* subsp. *contorta* is an occasional host.

Distribution: *Arceuthobium siskiyouense* is common in the Klamath Ranges in Del Norte County and western Siskiyou County.

Diagnostic Characters: **Plants** 5–17 cm tall (mean 9), usually reddish-brown, but some staminate plants may be yellow-brown to green-brown. **Basal diameter** of dominant plants 1.8–6.1 mm (mean 3.1). **Staminate spike** length 5.2–19.1 mm (mean 11.8), 1.5–2.6 mm wide (mean 2). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2.5–3.9 mm in diameter (mean 3.2), 4-merous flowers 3.6–5.9 mm in diameter (mean 4.5). **Petals** 1.1–2.0 mm long (mean 1.5), 1–2.1

mm wide (mean 1.5), same color as plants. **Anther** diameter 0.4–1.2 mm (mean 0.8). **Fruits** 3.8–6.1 mm long (mean 5.2) and 2.5–4.3 mm wide (mean 3.4), light green and lightly glaucous. **Seeds** 2–4 mm long (mean 3.1) and 0.8–1.9 mm wide (mean 1.3). **Anthesis** begins in late July, peaks in mid August, and continues into early September. **Seed dispersal** starts in late September, peaks in mid to late October, and is completed by late November. See Hawksworth et al. (1992), Hawksworth and Wiens (1996, p. 241), Mathiasen and Daugherty (2013), and Mathiasen and Kenaley (2015a) for additional descriptions of this species.

14. *Arceuthobium tsugense* (Rosendahl) G. N. Jones subsp. *tsugense*

Western hemlock dwarf mistletoe

This dwarf mistletoe is rarely found in northern California near the Pacific Coast.

Hosts: *Tsuga heterophylla* (Raf.) Sarg. is the only host in California.

Distribution: This dwarf mistletoe is only known from two confirmed locations in California at present; east of Blue Lake on Route 299 (Humboldt County) and east of Mendocino (Mendocino County). However, this mistletoe is a common and damaging parasite of *T. heterophylla* in Oregon, Washington, Alaska, and British Columbia.

Diagnostic Characters: **Plants** 3–16 cm tall (mean 8), green, green-yellow, green-brown, purple. **Basal diameter** of dominant plants 1.3–5.5 mm (mean 2.7). **Staminate flowers** 3 or 4-merous, 3-merous flowers 1.8–4.7 mm in diameter (mean 3.2), 4-merous flowers 2.8–5.9 mm in diameter (mean 3.8). **Petals** 1–2.2 mm long (mean 1.5), 0.8–2.2 mm wide (mean 1.2), same color as plants. **Anther** diameter 0.3–1.3 mm (mean 0.7). **Fruits** 3.3–5.5 mm long (mean 4.4) and 2.2–3.5 mm wide (mean 2.9), light green. **Seeds** 1.8–3.5 mm long (mean 2.6) and 0.8–1.4 mm wide (mean 1.1). **Anthesis** begins in late July, peaks in August, and ends by late September. **Seed dispersal** is from late September to early November. See Hawksworth and Wiens (1996, pp. 243–244) for another description of this species.

15. *Arceuthobium tsugense* (Rosendahl) G. N. Jones subsp. *mertensianae* Hawksworth & Nickrent

Mountain hemlock dwarf mistletoe

This dwarf mistletoe can be identified by its green-brown shoots, which range in size from 2–5 cm and its parasitism of *Tsuga mertensiana* (Bong.) Carrière.

Hosts: *Tsuga mertensiana* is the principal host in California. This mistletoe also occurs on *Pinus monticola*, but usually just when this tree is growing near severely infected *T. mertensiana*. It has also been reported infecting *Picea breweriana* in the Klamath Ranges.

Distribution: This dwarf mistletoe is scattered in locally abundant populations from around Mosquito Lakes (Alpine County), west of Lake Tahoe (Alpine Meadows Ski Area, Placer County), in the vicinity of Gold Lake (Plumas County), in Mount Lassen National Park (Tehama County), and in a few widely scattered locations in the Klamath Ranges (Shasta and Siskiyou counties). It is also found in southern Oregon.

Diagnostic Characters: **Plants** 2–11 cm tall (mean 6), yellow-green, green-brown. **Basal diameter** of dominant plants 1–3.7 mm (mean 2). **Staminate flowers** 3 or 4-merous, 3-merous flowers 1.9–2.9 mm in diameter (mean 2.4), 4-merous flowers 2.4–3.8 mm in diameter (mean 3.1). **Petals** 0.8–1.5 mm long (mean 1.1), 0.7–1.3 mm wide (mean 1), same color as plants. **Anther** diameter 0.3–0.7 mm (mean 0.5). **Fruits** 3.8–4.8 mm long (mean 3.8) and 1.8–3.5 mm wide (mean 2.6), light green and slightly glaucous, often with purplish to reddish tip. **Seeds** 2.2–3.4 mm long (mean 2.8) and 0.8–1.4 mm wide (mean 1.1). **Anthesis** starts in early August, peaks in mid August to mid September, and is completed by early October. **Seed dispersal** occurs from mid August to mid September. See Hawksworth et al. (1992) and Hawksworth and Wiens (1996, pages 243–244 and 249) for additional descriptions of this species.

PHORADENDRON NUTTALL

Mistletoe

These mistletoes are obligate parasites of many woody trees in North America, but in California only three species are not host specific and instead parasitize several woody angiosperms. Four of the seven species of *Phoradendron* in California parasitize conifers in the Pinaceae or Cupressaceae. Although they are parasites, species of *Phoradendron* are not considered to be serious forest pathogens because they primarily absorb water and minerals from their hosts. However, severe infection can stress the host tree, particularly under drought conditions, and in some cases contribute to their premature death. These mistletoes can also reduce fruit production of severely infected trees.

Mistletoes in this genus are evergreen shrubs with stems usually larger than 25 cm. Leaves are opposite and either foliaceous or reduced to connate, deltoid scales. Plants are either glabrous or pubescent. Inflorescences are jointed, axillary,

or rarely terminal spikes. All of the species of *Phoradendron* in California are dioecious. Flowers have a 3-merous (2–4) calyx. Pistillate flowers are epigynous, with 1 style, a capitate stigma, an ovary with one chamber, and a calyx that is adnate to the ovary. *Phoradendron* fruits are a white, pink, or sometimes reddish drupe with one seed and a mucilaginous coating (viscin). The seeds are primarily dispersed by numerous species of birds.

FIELD KEY TO *PHORADENDRON* SPECIES IN CALIFORNIA

- 1. Leaves reduced to connate scales
 - 2. Stems canescent, especially at distal tip, reddish to green; pistillate inflorescence with 2–7 segments; primarily parasitic on leguminous shrubs and trees in desert regions . . . 1. *P. californicum*
 - 2'. Stems glabrous throughout, green to yellow green; pistillate inflorescence with 1–2 segments; parasitic on *Juniperus* or *Calocedrus decurrens* in mountain regions
 - 3. Parasite of *Juniperus*; internodes usually less than 1 cm long; plants usually remaining erect 3. *P. juniperinum*
 - 3'. Parasite of *Calocedrus decurrens*; internodes usually over 1 cm long; plants often becoming pendulous 4. *P. libocedri*
- 1'. Leaves not reduced to connate scales
 - 4. Leaf length usually >20 mm; stems usually with hairs; staminate inflorescence with 2–7 segments; pistillate inflorescence with 6–24 flowers; parasites of woody dicots
 - 5. Primarily a parasite of *Quercus*, but also on other hardwoods; leaves obovate-elliptic, 15–45 mm long, 10–22 mm wide; inflorescences densely stellate; staminate inflorescence with 2–4 segments, usually with 15–45 flowers; pistillate inflorescence usually with 2–3 segments and usually with 7–24 flowers; flowering July–September 7. *P. villosum*
 - 5'. Parasite of woody dicots other than *Quercus*; leaves obovate to elliptic-orbicular, 23–42 mm long, 15–29 mm wide; inflorescences usually glabrous; staminate inflorescence with 2–7 segments, usually with 15–60 flowers; pistillate inflorescence with 2–5 segments and usually with 6–20 flowers; flowering December–March 5. *P. macrophyllum*
 - 4'. Leaf length usually <20 mm; stems glabrous; staminate inflorescence usually with one segment; pistillate inflorescence with 2 flowers; parasites of *Juniperus*, *Cupressus*, or *Abies concolor*
 - 6. Parasite of *Juniperus* or *Cupressus*; leaves 10–20 mm long and 2–5 mm wide; staminate inflorescence usually with less than 10 flowers 2. *P. densum*
 - 6'. Parasite of *Abies concolor*; leaves usually 5–25 mm long, 5–8 mm wide; staminate inflorescence usually with more than 10 flowers 6. *P. pauciflorum*

IDENTIFICATION OF *PHORADENDRON*
IN CALIFORNIA

1. *Phoradendron californicum* Nuttall

Desert mistletoe

Phoradendron californicum is the common mistletoe found on *Prosopis* L. and *Parkinsonia* L. (and other trees and shrubs in the Fabaceae) in the Mojave and Sonora Deserts of the Southwest and northwestern Mexico. Because of its relative host specificity, scale-like leaves, and geographic distribution in desert ecosystems this mistletoe is easily identified.

Hosts: Common on leguminous trees and shrubs, particularly *Prosopis*, *Parkinsonia*, *Acacia*, and *Olneya*.

Distribution: This mistletoe is common in the Mojave Desert of southeastern California; it is found from Inyo County south into Baja California, Mexico. It is also common in the Sonora Desert of Arizona and northern Mexico.

Diagnostic Characters: **Plants** forming large, pendulous clumps, often over a meter in diameter, internodes 13–28 mm long (mean 20), 1–2.5 mm wide (mean 1.7), red to green, whitish canescent to subglabrous. **Leaves** ca. 1 mm long;

inflorescence moderately whitish canescent. **Staminate inflorescence** with 1–6 segments (mean 3), individual segments with 4–10 flowers (mean 6). **Anthesis** occurs from December to March. **Pistillate inflorescence** with 1–7 segments (mean 3), individual segments with 2–6 flowers (mean 3). **Fruits** white to red, 3 mm in diameter, essentially glabrous, mature during the winter. See Wiens (1964, p. 31) for another description of this species.

2. *Phoradendron densum* Trelease

Dense mistletoe

Hosts: This mistletoe parasitizes several species of *Juniperus* and *Cupressus*. Known hosts include *Juniperus californica* Carrière, *J. occidentalis* Hooker, *J. osteosperma* (Torrey) Little, *Cupressus arizonica* E. Greene, *C. bakeri* Jepson, *C. forbesii* Jepson, *C. goveniana* Gordon, *C. macnabiana* A. Murray, *C. macrocarpa* Gordon, and *C. sargentii* Jepson.

Distribution: *Phoradendron densum* occurs throughout California on *Juniperus* and *Cupressus*. It displays a very dense habit, hence the common name. It has small (about 14 × 4 mm), oblong, sessile leaves with rounded tips. *Phoradendron densum* should not be confused with the other

common mistletoe on *Juniperus* in California, *P. juniperinum*, because the latter mistletoe has leaves that are reduced to connate scales and appears to be "leafless."

Diagnostic Characters: **Plants** forming dense clumps of branches up to a meter in diameter, but usually about 30–50 cm in height, internodes 6–17 mm long (mean 11), 1.5–2 mm wide (mean 1.7), typically green, glabrous. **Leaves** typically oblanceolate, sessile, 10–20 mm long (mean 14), 2–5 mm wide (mean 3), apex usually obtuse. **Staminate inflorescence** with 1–2 segments, individual segments with 6–13 flowers (mean 8). **Anthesis** approximately from late May to mid August. **Pistillate inflorescence** with 1–2 segments, individual segments with 2 flowers. **Fruits** white to lightly pink, 4 mm in diameter, mature in the winter. See Wiens (1964, p. 29) and Wiens and Hawksworth (2002) for additional descriptions of this species.

3. *Phoradendron juniperinum* A. Gray

Juniper mistletoe

Hosts: This mistletoe only parasitizes *Juniperus* throughout California.

Distribution: *Phoradendron juniperinum* is common on *Juniperus* in California. Its scale-like leaves and pink to white berries that are mature in winter easily identify this mistletoe. Like other species of *Phoradendron* birds disseminate its seeds.

Diagnostic Characters: **Plants** forming dense clumps of branches up to 60 cm in diameter, stems woody at their base when mature, glabrous, internodes 5–12 mm long (mean 8), 1.5–2.5 mm wide (mean 1.8), typically green, but some plants appearing yellow-green or almost brown. **Leaves** reduced to scales about 1 mm long, often finely ciliate. **Staminate inflorescence** with 1–2 segments, individual segments with 5–9 flowers (mean 7). **Anthesis** is approximately from July through September. **Pistillate inflorescence** with 1 segment with 2 flowers. **Fruits** pinkish white, 4 mm in diameter, glabrous, mature in the winter. See Wiens (1964, p. 22) for another description of this species.

4. *Phoradendron libocedri* (Engelmann) Howell

Incense cedar mistletoe

Hosts: This mistletoe only parasitizes *Calocedrus decurrens* (Cupressaceae) in California and southern Oregon.

Distribution: *Phoradendron libocedri* is common in California wherever *Calocedrus decurrens* grows. Thus far, it has not been reported to parasitize *Juniperus*. However, *P. libocedri* is easily distinguished from *P. juniperinum* by its longer internodes, pendulous habit, and, as

noted, exclusive parasitism of *Calocedrus decurrens*.

Diagnostic Characters: **Plants** forming dense clumps of branches up to 80 cm in diameter, stems woody at their base when mature, glabrous, internodes 8–20 mm long (mean 13), 1–2 mm wide (mean 1.5), typically dark green, often pendulous. **Leaves** reduced to scales about 1 mm long, often finely ciliate. **Staminate inflorescence** with 1–2 segments, individual segments with 5–9 flowers (mean 7). **Anthesis** is approximately from July through September. **Pistillate inflorescence** with 1 segment with 2 flowers. **Fruits** pinkish white, 4 mm in diameter, glabrous, mature in the winter. See Wiens (1964, p. 24) for another description of this species.

5. *Phoradendron macrophyllum* (Engelmann) Cockerell

Big leaf mistletoe

Phoradendron macrophyllum is a common parasite of a wide variety of hardwood trees from central California south to northern Mexico and east across southern Arizona and New Mexico into western Texas. It has large, smooth leaves that may be as long and wide as 50 × 30 mm. This is the common mistletoe on willows and cottonwoods along drainages throughout its wide geographic range. This is the mistletoe on *Juglans* and other hardwoods in the orchards and cities of the Great Central Valley. *Phoradendron macrophyllum* has nearly smooth stems (few, if any hairs) while those of *P. villosum* (number 7 below)—a principal parasite of *Quercus*—have obviously hairy stems.

Hosts: *Phoradendron macrophyllum* is reported to parasitize over 70 species of hardwood trees in over 30 genera. It has one of the largest host ranges of any *Phoradendron* in the United States. Therefore, a large, leafy mistletoe observed on a hardwood in California will most often be *P. macrophyllum*. It is rare on *Quercus* in California; the mistletoe common on *Quercus* throughout California is *P. villosum* (see number 7 below).

Distribution: *Phoradendron macrophyllum* is found from the Great Central Valley of California (Butte County) south in the Coast Ranges and foothills of the Sierra Nevada to southern California and northern Mexico. It then ranges east across the Mojave Desert into central Arizona south of the Mogollon Rim and then across the Sonora Desert into southern New Mexico. It is common along the Rio Grande River in southern New Mexico south into west Texas.

Diagnostic Characters: **Plants** forming dense clumps of branches up to a meter in diameter, stems woody at their base when mature, green, usually glabrous, internodes 22–59 mm long

(mean 36), 1.5–3 mm wide (mean 2.1), typically dark green or yellow-green. **Leaves** obovate, elliptic-orbicular, 23–42 mm long (mean 31), 15–30 mm wide (mean 20). **Staminate inflorescence** with 2–7 segments (mean 4), individual segments with 15–60 flowers (mean 34). **Anthesis** is approximately from December through March. **Pistillate inflorescence** with 2–5 segments (mean 3), each segment with 6–20 flowers (mean 11). **Fruits** distinctly white, 4–5 mm in diameter, glabrous, mature in the winter. See Wiens (1964, p. 41) under *P. tomentosum* subsp. *macrophyllum* for another description of this species.

6. *Phoradendron pauciflorum* Torrey

Fir mistletoe

Phoradendron pauciflorum is a common parasite of *Abies concolor* especially in the Sierra Nevada. It has long, spatula-shaped leaves and is the only *Phoradendron* that occurs on *A. concolor*, so it is easily identified.

Hosts: This mistletoe is only known to parasitize *Abies concolor*.

Distribution: *Phoradendron pauciflorum* occurs from the central Sierra Nevada (Calaveras County) to southern California in the San Bernardino, San Gabriel, San Jacinto, and Laguna Mountains. It also occurs in the Santa Catalina and Rincon Mountains of southern Arizona and the Sierra San Pedro Mártir of Baja California, Mexico.

Diagnostic Characters: **Plants** forming dense clumps up to 70 cm in diameter, stems woody at their base when mature, green, glabrous, internodes 10–21 mm long (mean 15), 1.5–2.5 mm wide (mean 2). **Leaves** subpetiolate, usually oblanceolate, 5–25 mm long (mean 20) and 5–8 mm wide (mean 6), apex acute-obtuse. **Staminate inflorescence** with 1–2 segments, individual segments with 6–14 flowers (mean 10). **Anthesis** is approximately from July through September. **Pistillate inflorescence** with 1 segment with 2 flowers. **Fruits** white, glabrous, 4 mm in diameter, mature in the winter. See Wiens (1964, p. 30) and Wiens and Hawksworth (2002) for additional descriptions of this species.

7. *Phoradendron villosum* (Nuttall) Nuttall

Oak mistletoe

This mistletoe is easily identified by its whitish to yellowish pubescence, its large, fleshy to leathery leaves, and common parasitism of *Quercus*. Some trees have many mistletoe plants and these can easily be observed during the winter when leaves are off the host, but remain on the mistletoe plants. Birds disseminate the mistletoe seeds.

Hosts: This mistletoe is primarily a parasite of *Quercus*, but has also been reported on other hardwood hosts in California.

Distribution: *Phoradendron villosum* is common on *Quercus* in and around the Great Central Valley, in the southern Sierra Nevada, and in the South Coast Ranges. It is also common in Oregon.

Diagnostic Characters: **Plants** up to one meter in diameter; most parts covered with whitish or yellowish pubescence; stems woody at maturity, internodes 15–38 mm long (mean 24), 1–3 mm wide (mean 2.1), typically gray-green or yellow-green. **Leaves** very densely pubescent, obovate-elliptic, often thick and leathery, 15–45 mm long (mean 27), 10–22 mm wide (mean 15). **Inflorescences** densely stellate. **Staminate inflorescence** with 2–4 segments, individual segments usually with 15–45 flowers (mean 29). **Anthesis** occurs from July through September. **Pistillate inflorescence** with 2–3 segments, individual segments usually with 7–24 flowers (mean 13). **Fruits** white to pink, about 3–4 mm in diameter, puberulent just below the calyx, mature in the late fall to winter. See Wiens (1964, p. 44) for another description of this species.

VISCUM

European Mistletoe

1. *Viscum album* L.

European Mistletoe

Only *Viscum album* occurs in California, and was purposely introduced to Sebastopol by Luther Burbank around 1900.

Hosts and Distribution: Parasitic on several genera of deciduous trees, including fruit trees, in Sonoma County (vicinity of Sebastopol and Santa Rosa).

Diagnostic Characters: *Viscum album* is a dioecious evergreen shrub with stems that are usually >20 cm tall, round, and green or less often reddish. **Branches** are opposite or sometimes whorled. **Leaves** are usually 5–8 cm long and about 1.5 cm wide, narrow obovate, with a short petiole. The **inflorescence** is a cyme, with few flowers formed on short or sessile peduncles that are subtended by a pair of fused bracts. **Flower parts** are in fours and anthers have several chambers. **Pistillate flower parts** are deciduous. **Fruits** are 6–10 mm in diameter, spheric, and on a short pedicel, white and they mature during the winter.

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APPENDIX 1. Identification of mistletoes in California using common hosts and geographic location.¹

Host	Location	Mistletoe
Haploxyton Pines (soft pines)²		
<i>Pinus albicaulis</i> (Whitebark pine)	Mt. Shasta, Mt. Eddy	<i>Arceuthobium</i>
<i>Pinus balfouriana</i> ³ (Foxtail pine)	Mt. Eddy	<i>A. cyanocarpum</i>
<i>Pinus edulis</i> (Colorado pinyon pine)	Clark and New York Mtns.	<i>A. cyanocarpum</i>
<i>Pinus flexilis</i> (Limber pine)	East side of the Sierra Nevada, San Bernardino, and San Jacinto Mtns.	<i>A. divaricatum</i>
<i>Pinus lambertiana</i> ⁴ (Sugar pine)	Near Orleans, south to the North Coast Range, Mt. Lassen south on the west side of the Sierra Nevada to the Cuyamaca Mtns. in San Diego County	<i>A. cyanocarpum</i>
<i>Pinus monophylla</i> (Singleleaf pinyon pine)	East side of the Sierra Nevada, Mojave Desert Mtns., and Transverse Ranges	<i>A. divaricatum</i>
<i>Pinus monticola</i> (Western white pine)	Klamath Ranges	<i>A. monticola</i>
<i>Pinus quadrifolia</i> (Parry pinyon pine)	Mt. Shasta, Mt. Eddy	<i>A. cyanocarpum</i>
Diploxyton Pines (hard pines) ²	Laguna Mtns.	<i>A. divaricatum</i>
<i>Pinus attenuata</i> (Knobcone pine)	Klamath Ranges	<i>A. siskiyouense</i>
<i>Pinus contorta</i> subsp. <i>murrayana</i> (Lodgepole pine)	All other regions	<i>A. campylopodum</i>
<i>Pinus coulteri</i> (Coulter pine)	Modoc Plateau south through the Cascade Ranges and Sierra Nevada to the San Bernardino Mtns.	<i>A. americanum</i>
<i>Pinus jeffreyi</i> ⁵ (Jeffrey pine)	Transverse and Peninsular Ranges	<i>A. campylopodum</i>
<i>Pinus muricata</i> (Bishop pine)	Klamath Ranges	<i>A. siskiyouense</i>
<i>Pinus ponderosa</i> ⁶ (Ponderosa pine)	North Coast Ranges, Klamath Ranges east and south through the Sierra Nevada, Transverse Ranges, and south to the Laguna Mtns.	<i>A. campylopodum</i>
<i>Pinus radiata</i> (Monterey pine)	North Coast north of San Francisco to near Fort Bragg	<i>A. littorum</i>
<i>Pinus sabiniana</i> ⁷ (Gray pine)	North Coast Ranges, Klamath Ranges, east and south through the Sierra Nevada to the Transverse Ranges, and Laguna Mtns.	<i>A. campylopodum</i>
Other Common Hosts		
<i>Abies concolor</i> ⁸ (White fir)	Central Coast south of San Francisco to near Cambria	<i>A. littorum</i>
<i>Abies grandis</i> (Grand fir)	Foothills of the Coast Ranges and Sierra Nevada, and the Transverse Ranges (north slope)	<i>A. occidentale</i>
<i>Abies magnifica</i> (Red fir)	Klamath and Cascade Ranges, Sierra Nevada, and the San Bernardino Mtns.	<i>A. abietinum</i> f. sp. <i>concoloris</i>
	Klamath Ranges and the North Coast Ranges	<i>A. abietinum</i> f. sp. <i>concoloris</i>
	Sierra Nevada	<i>A. abietinum</i> f. sp. <i>magnificae</i>
	Klamath Ranges and South Fork Mountain	<i>A. abietinum</i> subsp. <i>wiensii</i>

APPENDIX 1. CONTINUED

Host	Location	Mistletoe
<i>Picea breweriana</i> (Brewer spruce)	Klamath Ranges	<i>A. abietinum</i> subsp. <i>wiensii</i>
<i>Pseudotsuga menziesii</i> (Douglas fir)	Klamath Ranges, North Coast Ranges, Mt. Shasta, and Mt. Lassen	<i>A. monticola</i>
<i>Tsuga heterophylla</i> (Western hemlock)	North Coast Ranges	<i>A. douglasii</i>
		<i>A. tsugense</i> subsp. <i>tsugense</i>
<i>Tsuga mertensiana</i> (Mountain hemlock)	Klamath Ranges, Mt. Shasta, Mt. Lassen, and northern High Sierra Nevada	<i>A. tsugense</i> subsp. <i>mertensianae</i>
<i>Juniperus</i> (Junipers)		<i>Phoradendron</i>
<i>Juniperus</i> and <i>Cupressus</i> (Junipers and cypresses)		<i>P. juniperinum</i>
<i>Libocedrus decurrens</i> (Incense cedar)	East side of the Cascade Ranges, along the east side of the Sierra Nevada to the San Bernardino Mtns. and Desert Mtns.	<i>P. densum</i>
<i>Abies concolor</i> ⁸ (White fir)	Klamath Ranges and Coast Ranges, west side of the Sierra Nevada, Transverse Ranges, and Desert Mtns.	<i>P. libocedri</i>
<i>Quercus</i>	Throughout California	<i>P. pauciflorum</i>
Leguminous Trees/Shrubs	Coast Ranges to San Diego County	<i>P. villosum</i>
Hardwoods other than <i>Quercus</i>	Throughout California	<i>P. californicum</i>
	Mojave and Sonora Desert	<i>P. macrophyllum</i>
	Central to southern California	<i>Viscum</i>
Hardwoods including <i>Acer</i> , <i>Betula</i> , <i>Malus</i> , <i>Populus</i> , <i>Prunus</i> , <i>Pyrus</i> , and <i>Ulmus</i>	Sonoma County (Santa Rosa-Sebastopol)	<i>V. album</i>

¹ Appendix 1 is not designed for the identification of mistletoes in California using herbarium specimens, unless both the host and geographic location are clearly indicated on the herbarium label.

² *Pinus* is subdivided into two subgenera: subgenus *Strobus*, which are also known as haploxyton or soft pines, and subgenus *Pinus*, which are also referred to as diploxyton or hard pines. Haploxyton pines have one vascular bundle per needle while diploxyton pines have two vascular bundles per needle.

³ In the Mount Eddy area (Siskiyou County) *Pinus balfouriana* is only an occasional host of *Arceuthobium cyanocarpum*.

⁴ *Pinus lambertiana* is occasionally infected by *Arceuthobium abietinum* f. sp. *concoloris* in forests where there is also severe infection on *Abies concolor* by this dwarf mistletoe.

⁵ In the Klamath Ranges *Arceuthobium siskiyouense* and *A. campylopodium* occasionally occur in the same area and both can infect *Pinus jeffreyi*. At these locations, it is necessary to carefully examine the staminate spikes of male plants; the spikes of *A. siskiyouense* are about 2 mm wide and those of *A. campylopodium* are about 3 mm in width. *Pinus jeffreyi* is occasionally infected by *A. americanum*, but only in areas where there is also severe infection on *Pinus contorta* by this dwarf mistletoe.

⁶ *Pinus ponderosa* may be occasionally infected by *Arceuthobium americanum* and *A. occidentale* in the Sierra Nevada.

⁷ *Pinus sabiniana* is occasionally infected by *Arceuthobium campylopodium* on the west side of the Sierra Nevada.

⁸ Here we classify white fir as *Abies concolor*, which includes *Abies concolor* var. *lowiana* (Gordon) Lemmon.

GENOMIC AND PHYLOGENETIC ANALYSIS OF THE COMPLETE PLASTID GENOME OF THE CALIFORNIA ENDEMIC SEAWEED *WILDEMANIA SCHIZOPHYLLA* (BANGIACEAE)

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ABSTRACT

Recent genetic studies of the Bangiales (Rhodophyta) led to the resurrection of the marine red algal genus *Wildemanian* De Toni. To gain a better understanding of the phylogenetic history of this genus and its plastid genome structure, the holotype specimen of *Wildemanian schizophylla* (Hollenberg) S. C. Lindstrom was analyzed using next generation sequencing technology. The plastid genome of *W. schizophylla* is 193,008 bp in length and contains 249 genes, including 47 ribosomal, 34 tRNA, 29 photosystem, 27 open reading frames, 25 hypothetical proteins, 10 phycobiliprotein, 8 ATP synthase, and 8 cytochrome b/f complex genes. The plastid genome shows similar organization and content to other Bangiaceae, except that it lacks the typical 16S and 23S ribosomal RNA repeat. Phylogenetic analysis of the *W. schizophylla* plastid genome against other Bangiaceae places *W. schizophylla* in a robustly supported position, intermediate between *Porphyra* C. Agardh and *Pyropia* J. Agardh. These data support the recent resurrection of the genus *Wildemanian*. Plastid genome analysis of the holotype specimen of *W. schizophylla* generated an authentic barcode that can be used for future taxonomic studies. Comparison of the *rbcL* sequence from the type material of *W. schizophylla* confirms it is endemic to California.

Key Words: Bangiaceae, holotype, phylogenetic, plastid genome, red algae, *Wildemanian*.

The Bangiaceae is a predominantly marine red algal family with approximately 150 species distributed worldwide (Sutherland et al. 2011). The family includes the economically important *nori* (Mumford and Miura, 1988). Species in the Bangiaceae were traditionally classified into two genera based on their morphology. Filamentous representatives were placed in *Bangia* Lyngbye and foliose thalli were organized into *Porphyra* C. Agardh. Based on recent phylogenetic analyses using small subunit ribosomal RNA (SSU) and large subunit ribulose-1,5-biphosphate carboxylase/oxygenase (*rbcL*) DNA sequences, the taxonomy of the Bangiales was restructured to recognize seven filamentous and eight foliose genera (Sutherland et al. 2011). In the Pacific Northwest, the majority of the foliose species previously classified as *Porphyra* were sorted to *Pyropia* J. Agardh, a resurrected genus containing more than 75 marine taxa. Several species however were reassigned to *Wildemanian* De Toni, a lesser known genus accommodating at least seven species with primarily distromatic and reddish pink thalli that inhabit the low intertidal and subtidal zones (Sutherland et al. 2011). To test the generic distinctness of the newly recognized *Wildemanian* from other Bangiaceae, Silva and Hughey (2014) analyzed the complete mitogenome of *W. schizophylla*. Compared to the mitogenomes of other Bangiaceae, they found that gene synteny was conserved, but that the genome was significantly smaller. They concluded

that *Wildemanian* was distinct from *Porphyra*. A complete plastid genome from a representative of the genus *Wildemanian* has yet to be determined and compared to *Porphyra* and *Pyropia*.

To gain further insight into Bangialean plastid genome structure and the phylogenetic position of *Wildemanian*, next generation sequencing methods were employed to generate genomic data from the holotype specimen of the native California seaweed *Wildemanian schizophylla* (Hollenberg) S. C. Lindstrom (Basionym: *Porphyra schizophylla* Hollenberg in Smith & Hollenberg, 1943 p. 213). *Wildemanian schizophylla* accommodates yellowish to light brownish-purple plants with distromatic thalli that have a conspicuous line of separation between the two layers of cells (Smith and Hollenberg 1943). The type material of *W. schizophylla* was collected from rocks swept by heavy surf at the high-tide level from Pescadero Point, Carmel. The resulting data was used to assemble the complete plastome for taxonomic, phylogenetic, and genomic analysis within the Bangiaceae.

MATERIALS AND METHODS

The DNA extraction was performed following the protocol outlined in Lindstrom et al. (2011) and the precautionary guidelines proposed by Hughey and Gabrielson (2012). The genome library was constructed and analyzed using Proton Ion sequencing by HTGC (<http://www.htseq.org/>)

TABLE 1. Plastid gene content for the holotype specimen of *Wildemania schizophylla*.

Gene groups	Genes
Photosystem I	psaA, psaB, psaC, psaD, psaE, psaI, psaF, psaJ, psaK, psaL, psaM
Photosystem II	psbA, psbB, psbC, psbD, psbE, psbF, psbH, psbI, psbJ, psbK, psbL, psbN, psbT, psbV, psbW, psbX, psbY, psbZ
Protochlorophyllide reductase	chlL, chlN, chlB, chlI-2
Phycobiliproteins	apcA, apcB, apcD, apcE, apcF, cpeA, cpeB, cpcA, cpcB, cpcG
Cytochrome b/f complex	petA, petB, petD, petF, petG, petJ, petL, petN
ATP synthase	atpA, atpB, atpD, atpE, atpF, atpG, atpH, atpI
RNA polymerase	rpoA, rpoB, rpoC1, rpoC2
Ribosomal proteins (SSU)	rps1, rps2, rps3, rps4, rps5, rps6, rps7, rps8, rps9, rps10, rps11, rps12, rps13, rps14, rps16, rps17, rps18, rps19, rps20
Ribosomal proteins (LSU)	rpl1, rpl2, rpl3, rpl4, rpl5, rpl6, rpl9, rpl11, rpl12, rpl13, rpl14, rpl16, rpl18, rpl19, rpl20, rpl21, rpl22, rpl23, rpl24, rpl27, rpl28, rpl29, rpl31, rpl32, rpl33, rpl34, rpl35, rpl36
Hypothetical chloroplast proteins	ycf3, ycf4, ycf12, ycf17, ycf19, ycf20, ycf21, ycf22, ycf23, ycf26, ycf28, ycf29, ycf31, ycf33, ycf34, ycf35, ycf36, ycf37, ycf38, ycf39, ycf46, ycf59, ycf61, ycf63, ycf65
Transfer RNAs	trnA-GGC, trnA-TGC, trnC-GCA, trnD-GTC, trnF-GAA, trnG-GCC, trnG-TC C, trnH-GTG, trnI-GAT, trnK-TTT, trnL-CAA, trnL-GAG, trnL-TAA, trnL-TAG, trnM-CAT(x3), trnN-GTT, trnP-TGG, trnQ-TTG, trnR-ACG, trnR-CCG, trnR-CCT, trnR-TCT, trnS-CGA, trnS-GCT, trnS-GGA, trnS-TGA, trnT-GGT, trnT-TGT, trnV-GAC, trnV-TAC, trnW-CCA, trnY-GTA
Ribosomal RNAs	rrsB, rrfA, rrfB, rrlB
Other genes	accA, accB, accD, acpP, argB, bas1, carA, cbbx, ccs1, ccsA, cemA, clpC, dnaB, dnaK, fabH, ftrB, ftsH, glbB, gltB, groEL, ilvB, ilvH, infB, infC, moeB, nb1A, odpA, odpB, ompR, pbsA, pgmA, preA, rbcL, rbcR, rbcS, rne, secA, secY, su fB, sufC, syfB, syh, tatC, thiG, trpA, trpG, trxA, tsf, tufa
Open reading frames	orf36, orf58, orf62, orf68, orf71(x2), orf75, orf107, orf108, orf111, orf114, orf121, orf148, orf149, orf174, orf198, orf203, orf238, orf240, orf263, orf287, orf320, orf327, orf382, orf450, orf565, orf621

following the manufacturer’s instructions (Life Technologies, Grand Island, NY). The 55,560,324 filtered reads were assembled using default denovo settings with CLC Cell 4.3.0 (©2015 CLC bio, a QIAGEN Company). The resulting contigs were searched at NCBI using Standard Nucleotide Blast, then the aligned contigs were arranged according to plastid reference sequences (*Py. yezoensis*- KC517072, *Py. haitanensis*- KC464603, and *Py. kanakaensis*- KJ776836). The remaining three gaps were closed via targeted PCR and direct Sanger sequencing as described in Lindstrom et al. (2011). The plastid features were annotated following the methods of Hughey et al. (2014), using NCBI ORF-finder and alignments obtained via BLASTX. The tRNAs were identified using the tRNAscan-SE 1.21 web server (Schattner et al. 2005), and rRNAs using the RNAmmer 1.2 server (Lagesen et al. 2007). Alignment of the plastid genomes was accomplished using MAFFT (Katoh and Standley 2013). Maximum likelihood analysis was performed using RaxML (Stamatakis 2014) with 1000 bootstrap replicates and default parameters in Galaxy (Giardine et al. 2005; Blankenberg et al. 2010; Goecks et al. 2010). Bayesian analysis was executed with MrBayes 3.2.1 (Huelsenbeck et al. 2001; Ronquist and Huelsenbeck 2003) using the search parameters described by Lindstrom et al.

(2015). *Porphyra purpurea* and *P. umbilicalis* were designated as outgroup taxa for both analyses. The phylogenetic trees were visualized with TreeDyn 198.3 at Phylogeny.fr (Dereeper et al. 2008). Pairwise distances were calculated using the default settings (GTR substitution model) with DIVEIN (Deng et al. 2010).

RESULTS

The complete plastid genome of *W. schizophylla* is 193,008 bp in length, AT rich (65.6%), and contains 249 genes (Table 1). The genes include 47 ribosomal proteins (small subunit-19, large subunit-28), 34 tRNA, 29 photosystem (photosystem I-11, photosystem II-18), 27 open reading frames, 25 hypothetical proteins, 10 phycobiliprotein, 8 ATP synthase, and 8 cytochrome b/f complex genes (Table 1).

Maximum likelihood and Bayesian phylogenetic analysis of the *W. schizophylla* plastome against five complete plastid sequences of *Pyropia* and two of *Porphyra*, resolves *W. schizophylla* in an intermediate position on the tree at the end of a long branch (Fig. 1). All branches on the tree received full support (bootstraps- 100, posterior probabilities- 1.0). Analysis of pairwise distances between *W. schizophylla* and representatives of *Porphyra* (26.6%–26.8%) and *Pyropia* (24.8%–27.5%)

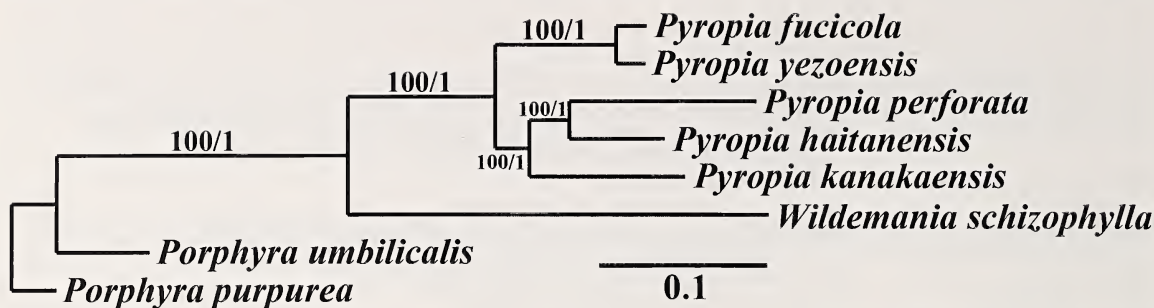


FIG. 1. Maximum likelihood phylogram of published Bangiaceae plastid genomes. Maximum likelihood bootstrap supports (nreps = 1000) and Bayesian posterior probabilities are listed left/right, respectively. The legend below represents the scale for nucleotide substitutions.

showed large distances. Distances between representatives of *Porphyras* and *Pyropia* ranged from 17.9 to 20.4%. Within genera, the two *Porphyras* species differed by 8.3%, and *Pyropia* by 3.4%–14.6%.

Standard Nucleotide Blast analysis of the *rbcL* gene sequence obtained from the holotype of *W. schizophylla* failed to yield an exact match. There are five specimens identified as *W. schizophylla* currently in the database (three of the five are listed as *P. schizophylla*). The most similar sequence to the holotype was a specimen from Carmel, Monterey County, California, differing by 2 bp out of 1282 bp (GenBank EU223182). A specimen from Mendocino Head, Humboldt County, California (EU223183), was the next closest, differing by 10 bp out of 1177 bp. The third specimen from Van Damme State Park, Mendocino County, California (GU319871), differed by 13 bp out of 1331 bp. A sequence from a specimen from Sitka, Alaska (AF452443), originally attributed to *P. schizophylla* by Lindstrom and Fredericq (2003) and later assigned to *W. norrisii* (V. Krishnamurthy) S. C. Lindstrom by Sutherland et al. (2011), differed by 28 bp out of 1392 bp from the holotype of *W. schizophylla*. The final sequence was obtained from a specimen identified as *P. schizophylla* by Lindstrom and Fredericq (2003) from Point No Point, Vancouver Island, British Columbia (AF452444). It differed from the type of *W. schizophylla* by 82 bp out of 1411 bp.

DISCUSSION

The plastid genome of *Wildemanian schizophylla* is comparable in length (193,008 bp) to those published for the Bangiaceae (Reith and Munholland 1995; Smith et al. 2012; Wang et al. 2013; Hughey et al. 2014). Bangiophyte plastomes range in size from 189,752 (*Py. perforata*- Hughey et al. 2014) to 195,597 bp (*Py. haitanensis*- Wang et al. 2013). The plastome of *W. schizophylla* is also comparable in gene number (249 genes) to other

Bangiaceae. *Pyropia perforata* contains 247 genes and *Py. yezoensis*, *Py. haitanensis*, two *Porphyras* species all contain 252 genes (Smith et al. 2012; Wang et al. 2013; Hughey et al. 2014). Wang et al. (2013) found that *Py. yezoensis* and *Py. haitanensis* shared two ORFs that were deleted in *P. purpurea* and *P. umbilicalis* (ORF32, ORF36). *Wildemanian schizophylla*, as well as *Py. perforata*, *Py. fucicola*, and *Py. kanakaensis* lack ORF32, but all contain ORF36 (Hughey et al. 2014). Wang et al. (2013) also identified a four base pair overlap in genes *carA* and ORF238 in *Py. yezoensis* and *Py. haitanensis*, but reported it absent in *Porphyras*. This overlap is present in *Py. perforata*, *Py. fucicola*, and *Py. kanakaensis* (Hughey et al. 2014), but absent in *W. schizophylla*. The unique feature of the plastome of *W. schizophylla* is that it contains a single copy of the 16S and 23S ribosomal RNAs, similar to *Py. perforata*, but *Py. perforata* also lacks the 5S repeat which *W. schizophylla* contains. This deletion was confirmed with targeted PCR and sequencing of the ribosomal RNA locus. In comparison to the evolutionarily advanced red algae, the Florideophyceae contain a single copy of the 5S, 16S, and 23S RNAs (Janouškovec et al. 2013). The genericity of *Wildemanian*, *W. amplissima* (Kjellman) Foslie, as well as other accepted species classified to the genus requires genome sequencing or targeted PCR analysis to determine if the 16S and 23S deletions are characteristic of the genus. The other Bangiophytes previously analyzed, including two species of *Porphyras* and four of *Pyropia*, contain two non-identical copies of the 5S, 16S, and 23S ribosomal genes.

Phylogenetic analysis of the complete plastid genome of *W. schizophylla* places it on a long branch situated approximately intermediate in position between *Porphyras* and *Pyropia* (Fig.1). A similar relationship was inferred based on nuclear SSU and *rbcL* sequence data (Sutherland et al. 2011). Comparison of the pairwise plastid genome distances also found ample genetic divergence between *Wildemanian* and the two Bangiophyte genera *Porphyras* and *Pyropia*. These

plastid genome data confirm the conclusions reached by Sutherland et al. (2011) and Silva and Hughey (2014), that *Wildeman* was distinct from *Porphyra* and *Pyropia*.

Interspecific sequence variation for the *rbcL* gene varies between red algal species. The original work by Freshwater and Rueness (1994) found that for the Gelidiales interspecific variation is 1.2% to 10.7%. For the Bangiaceae, interspecific variation ranges from 0.22% to 10.7% (Kucera and Saunders 2012). Based on the analysis of the *rbcL* sequence obtained from the holotype specimen of *W. schizophylla*, the data indicate that *W. schizophylla* is endemic to California. The results also confirm the conclusion reached by Lindstrom (2008), that there is a morphologically similar, undescribed species of *Wildeman* to the north of the Monterey Peninsula. The specimens from Mendocino (0.85%) and Humboldt counties (0.98%) in Northern California are above reported intraspecific values (0–0.37%) for the family (Kucera and Saunders 2012). This undescribed entity requires further investigation and valid publication. Examination of the *rbcL* sequence from the specimen from Point No Point, Vancouver Island, indicated that its high sequence divergence was due to poor sequence data. Comparison of a truncated clean portion of that data to the specimen identified as *W. norrisii* from Sitka, Alaska (Sutherland et al. 2011), found the two to be nearly identical in sequence.

CONCLUSIONS

Complete plastid genome analysis of *W. schizophylla* supports the continued recognition of the recently reinstated genus *Wildeman*. The plastid genome of *W. schizophylla* is similar in organization, length, and content to other Bangiaceae, except that it lacks the typical non-identical 16S and 23S ribosomal RNA repeat. Plastid genome analysis of the holotype specimen of *W. schizophylla* provides an authentic barcode on which new species can be identified and existing species can be positively identified through genetic markers or genome comparisons.

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A NEW, LARGE-FLOWERED VARIETY OF *EREMOCARYA*
MICRANTHA (BORAGINACEAE)

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ABSTRACT

Eremocarya (Boraginaceae), a resurrected segregate of the genus *Cryptantha*, has recently been recognized as containing two species: *E. lepida* and *E. micrantha*. These two species differ in nutlet shape, nutlet size, and features of the corolla, including limb width, presence or absence of a prominent yellow coloration at the fornicies of the corolla center, and, perhaps most importantly, presence or absence of distinctive “fornix bodies” at the corolla mouth. Here we present evidence for a large-flowered form of *E. micrantha* that we argue should be treated as a new taxonomic variety, which we call *E. micrantha* var. *pseudolepida*. In nutlet morphology, *E. micrantha* var. *pseudolepida* is very similar to *E. micrantha* var. *micrantha* and different from *E. lepida*. *Eremocarya micrantha* var. *pseudolepida* differs from *E. micrantha* var. *micrantha* and is similar to *E. lepida* in corolla limb diameter and in having a tendency to possess a prominent yellow coloration in the corolla throat. However, *E. micrantha* var. *pseudolepida* lacks the distinctive fornic bodies of *E. lepida*. This new variety of *E. micrantha* is generally geographically discrete and allopatric relative to *E. micrantha* var. *micrantha*, with virtually all known populations occurring in Baja California, Mexico, between approximately 28° and 32° north latitude. However, two contiguous populations of a large-flowered *E. micrantha* were discovered in southeastern Arizona. In addition, one population of *E. micrantha* var. *pseudolepida*, in the central part of its range in Baja California, appears to be sympatric with a disjunct population of *E. micrantha* var. *micrantha*. We feel that the morphological distinctiveness and near geographic discontinuity of this entity warrants its status as a new taxon. Future molecular studies will be needed to evaluate the phylogeographic history of this intriguing complex of plants in order to evaluate both character evolution and taxonomic delimitation.

Key Words: Boraginaceae, *Cryptantha micrantha*, *Eremocarya lepida*, *Eremocarya micrantha*, *Eremocarya micrantha* var. *micrantha*, *Eremocarya micrantha* var. *pseudolepida*, fornic bodies, taxonomy.

Eremocarya Greene (Boraginaceae), a resurrected segregate of the genus *Cryptantha* Lehm. ex G. Don (see Hasenstab-Lehman and Simpson 2012), has recently been recognized to comprise two species: *E. lepida* (A. Gray) Greene and *E. micrantha* (Torrey) Greene (Simpson et al. 2014). *Eremocarya lepida* differs from *E. micrantha* in having a significantly wider corolla limb and a significantly greater nutlet length, maximum nutlet width, and maximum nutlet width:apical nutlet width (Simpson et al. 2014). In addition, *Eremocarya lepida* always has prominent, yellow fornicies at the upper corolla throat and clusters of unique “fornix bodies,” which are tiny (ca. 0.1 mm long), transparent, stalked, ellipsoid, sac-like structures. In contrast, *E. micrantha* lacks any evidence of fornic bodies and generally lacks or has reduced fornicies. The two species also differ in distribution, elevation, and associated plant community/vegetation type (see Simpson et al. 2014).

In their 2014 study of *Eremocarya*, Simpson et al. stated that “[o]bservation of *Eremocarya micrantha* specimens from Baja California, Mex-

ico reveals some lower elevation populations with relatively large corollas, but lacking fornic bodies and having a nutlet morphology typical of this taxon, these identified as *E. micrantha* but not included in our quantitative analyses. These unusual populations will be the subjects of a future study.” In fact, the great majority of specimens from this region had previously been identified or annotated as *Cryptantha micrantha* (Torr.) I.M. Johnst. var. *lepida* (A. Gray) I.M. Johnst. (= *Eremocarya lepida*), but nutlet morphology and absence of fornic bodies convinced the authors that they belonged to *E. micrantha*.

After a detailed quantitative study of all specimens of *Eremocarya* from Baja California known by us, and of many specimens from adjacent regions (including mainland Mexico), we conclude here that this large-flowered form should be recognized as a new taxon (based on phenetic discontinuities; see Cronquist 1978, 1988), which we treat as a variety of *E. micrantha*. We choose the rank of variety (over subspecies) by convention, as variety is used for infraspecific taxa in the closely related genus *Cryptantha*

almost exclusively (see Hamilton and Reichard 1992 for a synopsis of concepts of infraspecific classification.)

TAXONOMIC TREATMENT

Eremocarya micrantha (Torrey) Greene var. **pseudolepida** M.G.Simpson, L.M.Simpson, & Rebman, var. nov. — Type (Fig. 1): MEXICO, BAJA CALIFORNIA, 24 km NW by air from turn off of HWY 1 to Bahía de los Angeles. (29.23787° N, 114.26573° W). Alt.: 515 m. [Note: latitude/longitude and elevation indicated on specimen labels.] Granitic boulder fields and associated flats with *Agave shawii* subsp. *goldmaniana*, *Acalypha californica*, *Bursera microphylla*, *Euphorbia tomentulosa*, *Fouquieria columnaris*, *Pachycereus pringlei*, *Stenocereus gummosus*. Roots staining the new paper purple. Benjamin T. Wilder 10-116, 19 March 2010. With Jon P. Rebman, Ian Andrew Happle, and Sara Isabel Enciso Contreras. (holotype: SD218101; isotypes: ARIZ408970, RSA782708-0013360).

Diagnosis: *Eremocarya micrantha* var. *pseudolepida* is similar to *E. micrantha* var. *micrantha* in vegetative morphology, inflorescence structure, and fruit nutlet size and shape, the former differing in having a corolla with a larger (1.5–3.8 mm) limb width, with prominent yellow fornicies. *Eremocarya micrantha* var. *pseudolepida* is similar to *E. lepida* in having a relatively large corolla limb diameter, the former differing in having smaller, acute nutlets and in lacking fornic bodies at the corolla mouth.

Paratypes (arranged alphabetically by collector. Note: latitude, longitude, and/or elevation that are estimated from specimen label locality information are indicated with an asterisk (*); otherwise, these are listed verbatim from label information. See Figs. 6–8 for map of localities.): MEXICO, BAJA CALIFORNIA; base of mesa, near Village of San Simon, overlooking plain and Bay of San Quintin, 31.53102*, –115.71678*, 1,000 m* elev., 24-Mar-1949, *Bacigalupi* 3059 (UC917090); 31 km south of Bahia San Luis Gonzaga, 29° 30', –114° 16', 100 m elev., 9-Mar-1973, *Carter* 5705 (UC1443877); Bahia de Los Angeles, talus slope north and south of village, 28.94373*, –113.56246*, 50–200 ft elev., 9-Feb-1963, *Cowan* 2266 (SD127080); km 35 San Felipe-Ejido Morelia, 30° 52', –115° 7', 470 m elev., 14-Mar-1995, *Delgadillo s.n.* (BCMEX011336, SD165073); Mina Desengaña, ca. 16 miles north of Punta Prieta, 29.18004*, –114.14174*, 1,600–2,000 ft elev., 30-Mar-1950, *Gentry* 8897 (ARIZ274028, DES00009191, SD86410); 3.5 miles south of Punta Prieta, 28.87567*, –114.13421*, 170 m* elev., 4-May-1939, *Harbison s.n.* (SD25137); 26 miles north of Punta Prieta, 29.27623*, –114.20582*, 560 m* elev., 5-May-1939,

Harbison s.n. (SD25138); in sandy wash, 36 miles west of Bahia de Los Angeles, 29.04959*, –113.94653*, 420 m* elev., 10-Mar-1979, *McLaughlin* 2063 (ARIZ215596); 27.2 miles west of junction of Mexico 3 at roadside cleared area by Mexico 3, 31.30272*, –115.42470*, 640 m* elev., 10-May-1980, *McLaughlin* 2463 (ARIZ239724); Sierra San Borja, 28° 45', –113° 36.5', 1,100 m elev., 28-Mar-1960, *Moran* 8112 (ARIZ158791, SD60715, UC298136); north of Cerro San Luis, 29° 19', –114° 7', 1,250 m elev., 2-Mar-1963, *Moran* 10317.5 (SD54531); Sierra San Pedro Martir, Rancho San Matias, 31° 17', –115° 33', 1,050 m elev., 6-May-1963, *Moran* 10859 (SD53783); outwash slope near the village, Bahia de Los Angeles, 28° 56', –113° 35', 10 m elev., 21-Feb-1966, *Moran* 12311 (ARIZ165392, SD65317); La Bocana, 28° 28', –113° 25', 250 m elev., 10-Mar-1966, *Moran* 12496 (SD65316); Rancho Las Palomas, 28° 13', –113° 26', 400 m elev., 17-Mar-1966, *Moran* 12717 (SD65315, UC1345885); 2 miles south of El Crucero, 29° 14', –114° 11', 530 m elev., 1-Feb-1973, *Moran* 19624 (SD92326); 8 miles northwest of Sauzalito, 30° 12', –115° 27', 350 m elev., 7-May-1973, *Moran* 20886 (SD88930); mouth of Arroyo Taraizo, 31° 20', –115° 25.5', 800 m elev., 1-May-1976, *Moran* 22958 (SD95519); Cañon el Saladito, 14 km southeast of San Vicente, 31° 14.75', –116° 8', 170 m elev., 11-Apr-1982, *Moran* 30352 (SD110836); 14 miles west of San Felipe and Rte 5 along the road to Santa Clara, 31° 2', –115° 8', 720 m elev., 11-Mar-1993, *Rebman* 1484 (BCMEX06250, SD137251); dirt road from Highway 1 just south of mile marker 171, then ca. 0.6 mile west, then along path ca. 500 feet northwest from dirt road, 29.77881, –114.78226, 623 m elev., 7-Mar-2015, *Simpson* 3847 (SDSU21205); head of San Matias Pass, Highway 3, 31° 8.5', –115° 30', 920 m elev., 19-Apr-1985, *Thorne* 60111 (SD124982); sandy fields 2.8 km east of Rancho Pénjamo, 29° 59', –115° 6', 300 m elev., 20-Apr-1958, *Turner* 20 (UC112443); La Bocana, 29.7167, –114.75, 300 m elev., 18-Mar-2003, *Vinton s.n.* (SD182664); San Felipe Valley, 28 miles northwest of San Felipe, 31° 8', –115° 15', 430 m* elev., 28-Mar-1973, *Webster* 18216 (SD95971); vicinity of Bahia de los Angeles ca. 4.0 miles south of Las Flores, 28° 47', –113° 34', 150 m* elev., 13-Feb-1962, *Wiggins* 262 (SD94536); between San Augustin and Rancho Cataviña, 31.82882*, –116.51687*, 730 m* elev., 13-Apr-1931, *Wiggins* 5311 (UC660809); 40 miles NE of Pozo Aleman, 28.05770*, –113.39243*, 340 m* elev., 28-Feb-1935, *Wiggins* 7813 (UC651114); El Potrero, about 10 miles south of Rancho San Jose (Melting's Ranch), 31.75653*, –116.23410*, 2,300 ft elev., 20-May-1941, *Wiggins* 10043 (UC718753); partially stabilized sand dunes 6 miles south of San Felipe, 30.91265*, –114.72640*, 40* m elev., 18-Mar-1960, *Wiggins*

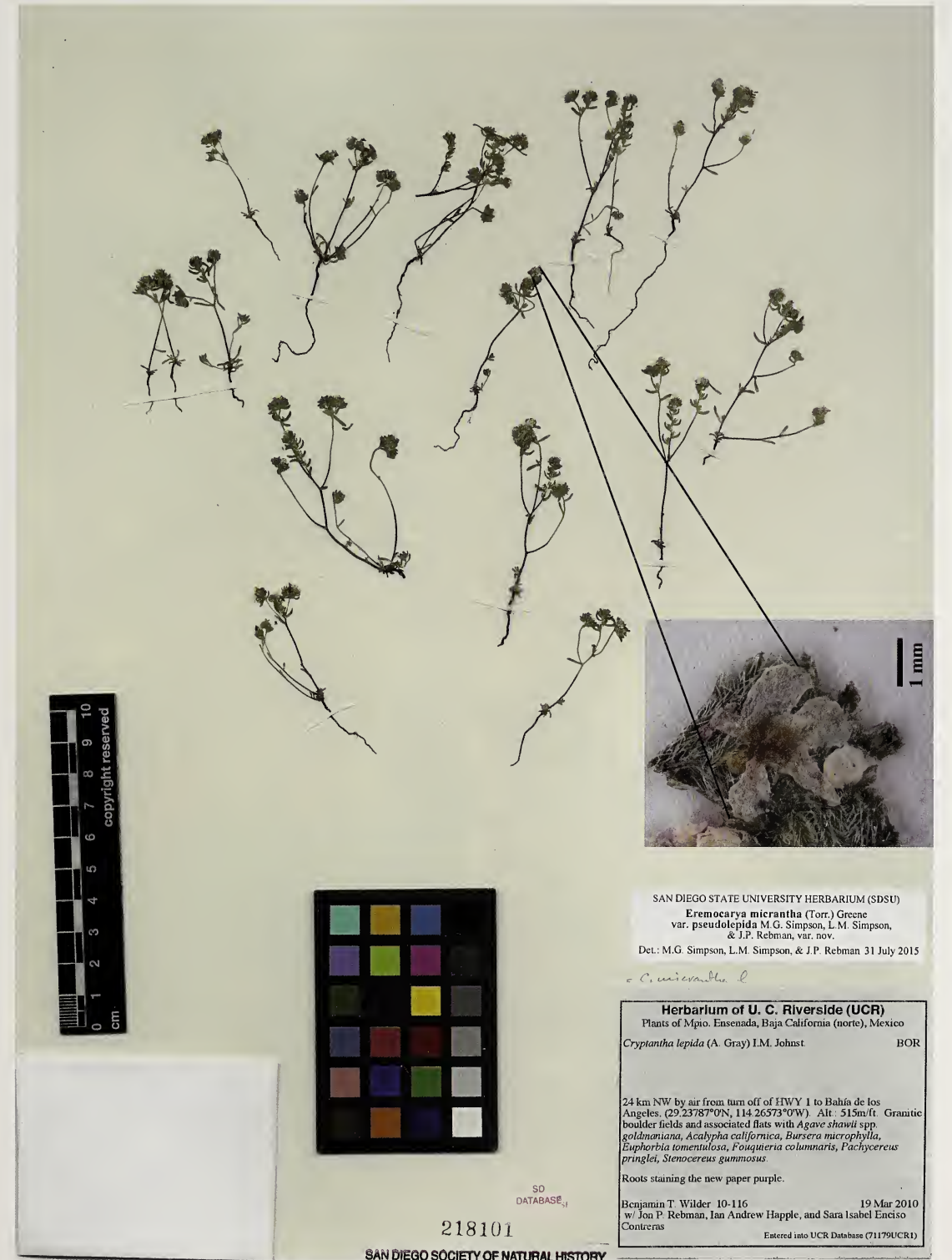


FIG. 1. Holotype specimen of *Eremocarya micrantha* var. *pseudolepida* (Wilder 10-116, SD218101). Inset shows magnified image of corolla.

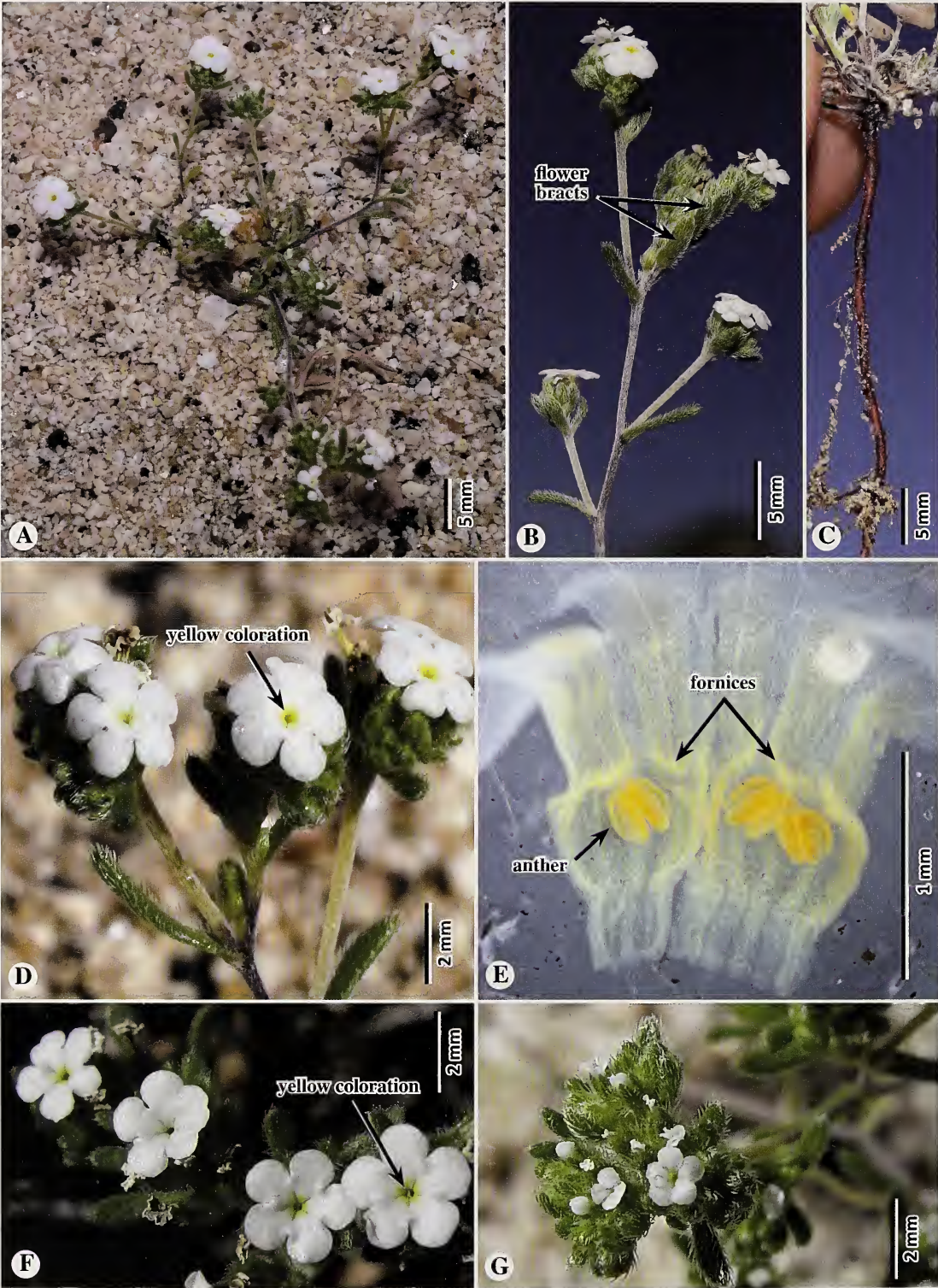


FIG. 2. A–E. *Eremocarya micrantha* var. *pseudolepida* (Simpson 3847, SDSU 21205). A–D. Field photographs, showing whole plant (A), floral bracts (B), red-pigmented root (C), and corollas with prominent yellow coloration at throat center D. E. Single flower longitudinally sectioned and opened, showing anthers (two detached) and inner surface of corolla tube with fornicies present but fornx bodies absent. F. *Eremocarya lepida* field photograph (Simpson 2816, SDSU17572), showing similarly large corollas with prominent yellow centers. G. *Eremocarya*

15799 (ARIZ169992, UC1303271); sandy bajada 2 miles NE of junction of Gulf road with western road, 20 miles N. of Punta Prieta, 29.27090*, -114.12354*, 700 m* elev., 16-Mar-1960, *Wiggins 15961* (ARIZ176981); sandy desert 18 miles north of Punta Prieta, 1/2 mile south of road to San Felipe, 29.23754*, -114.13853*, 600 m* elev., 26-Mar-1960, *Wiggins 15972* (ARIZ169970); granitic hillside 1.5 miles northwest of the village of Valle Trinidad, 31.4*, -115.7833*, 790 m* elev., 3-Apr-1960, *Wiggins 16067* (ARIZ169969); ca. 35 km E of El Rosario by air and ca. 5 km N by air of Hwy 1, 30° 7' 12.5", -115° 22' 20.8", 400 m elev., 22-Mar-2010, *Wilder 10-248* (ARIZ408961, SD218100, UCR) [Note: ARIZ and UCR specimens of *Wilder 10-248* are mixed collections of *Eremocarya micrantha* var. *pseudolepida* and *E. micrantha* var. *micrantha*].

We are excluding the following two Arizona populations as paratypes, given their disjunct distribution and ambiguous identity (see Discussion). Latitude/longitude of these two specimens were estimated from label locality information, indicated by asterisks (*); however, elevations were indicated on original labels. USA, ARIZONA, **Pima Co.**: annual, moist soil near streambed in riparian woodland, along Miller Creek, east side of the Rincon Mountains, 32.1576*, -110.4944*, 1,310 m elev., 18-Apr-1982, *Bowers R34* (ARIZ244153); annual, on dry, gravelly slopes in open pine-oak woodland, along Miller Creek, east side of the Rincon Mountains, 32.1600*, -110.4995*, 1,560 m elev., 1-May-1983, *Bowers R1152* (ARIZ243542).

Etymology. The varietal epithet means “false *lepida*,” because this new variety has most commonly been mistaken for *Eremocarya lepida* (= *E. micrantha* var. *lepida* (A. Gray) I.M. Johnst.; *Cryptantha micrantha* var. *lepida*; *C. m.* subsp. *lepida* (A. Gray) K. Matthew & P.H. Raven) because of its large corolla size.

MATERIALS AND METHODS

Field observations of all three taxa of *Eremocarya* were made and documented with photographs. Herbarium specimens were obtained and studied from the following herbaria: University of Arizona (ARIZ), Desert Botanical Garden (DES), San Diego Natural History Museum (SD), San Diego State University (SDSU), and University of California, Berkeley (UC). Acronyms of herbaria are after Thiers (continuously updated). A total of 216 herbarium specimens were sampled, annotated, and recorded for latitude/longitude and elevation (or these esti-

mated from label data). We concentrated our sampling on Mexico, California, and Arizona, with some in New Mexico and Nevada. A dried flower (the largest visible) from each specimen was boiled for 1–2 minutes and placed on a piece of clear, double-stick tape on a microscope slide. Corolla limb width of the boiled, re-expanded flower was measured with a video-interfaced dissecting microscope, using Image J software (Rasband 1997–2007, see Abramoff et al. 2004). (Our observations support the idea that re-expanded corollas are closer in dimensions to fresh flowers than are dried flowers, but we have no direct comparative measurements.) The corolla throat was then slit and opened, followed by staining with a drop of 0.5% toluidine blue. The presence or absence of corolla throat “fornix bodies” was observed and recorded.

From the same specimens, 2–3 mature fruits were detached and the nutlets removed and placed in dorsal (abaxial) view on the same microscope slide. The length, maximum width, and width at 1/4 relative distance from the apex were measured using the same apparatus. Nutlet data were segregated based on fruit heteromorphism. If selected fruits contained heteromorphic nutlets, the single (“odd”) large nutlet was tabulated separately from the three smaller (“consimilar”) nutlets, the latter values averaged. If fruit nutlets were homomorphic, measurements of all four were averaged. All measured nutlet parameters were averaged per herbarium specimen.

To visualize character distributions by taxon, box plots showing the median and the four quartiles of distribution were prepared for all three taxa for: (1) corolla limb width (mm); (2) nutlet length (mm); (3) nutlet maximum width (mm); and (4) the ratio of nutlet maximum width:width 1/4 from apex (see Simpson et al. 2014). For specimens with heteromorphic nutlets, only the largest nutlet was tabulated in these comparisons (see also Simpson et al. 2014). In addition, the extrinsic character of elevation was plotted (not illustrated). Each of these variables was evaluated for statistical difference (at probabilities <0.05 and <0.01) using analysis of variance (ANOVA), with multiple comparisons made between the taxon means using the Tukey post hoc test. Taxa that were statistically different from all other taxa in a particular character are indicated as such (at probabilities <0.01) in illustrated box plot diagrams. Note that the two large-flowered Arizona populations were omitted from these calculations because of their uncertain taxonomic status; however, the values of these specimens were indicated on the boxplots.

←

micrantha var. *micrantha* field photograph (Simpson 3126, SDSU19604), showing small corollas, generally with white or obscurely yellow centers.

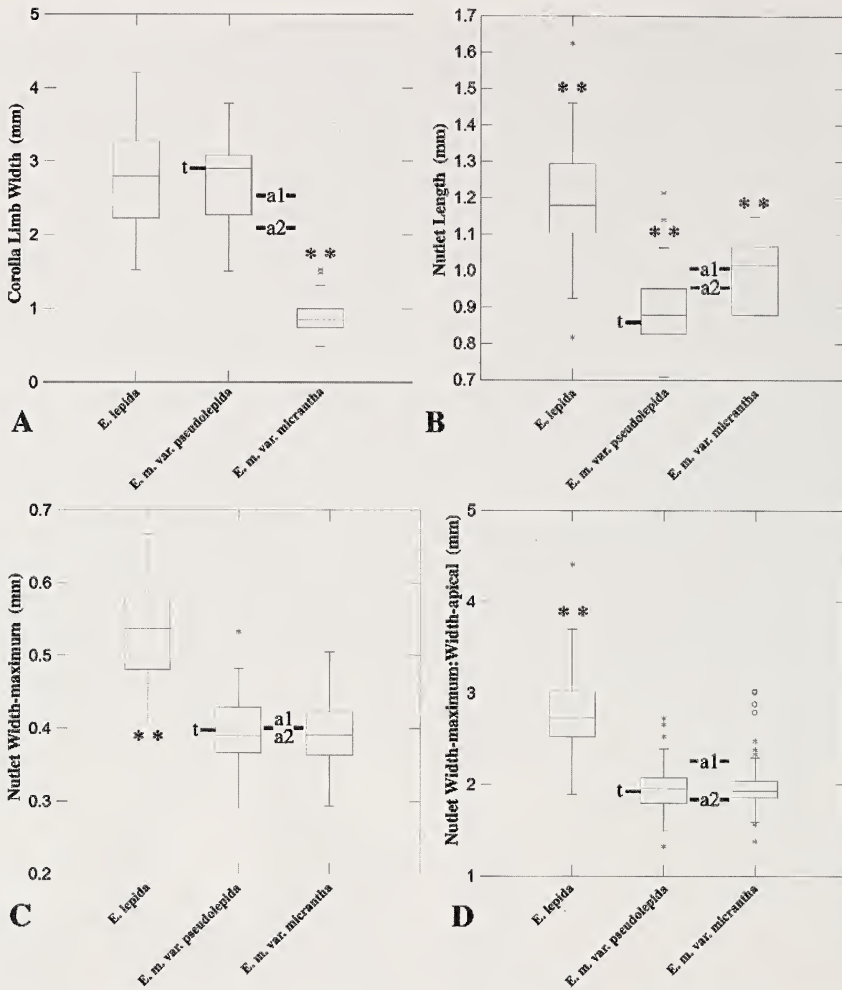


FIG. 3. Box plots of single characters analyzed for *E. lepida*, *E. micrantha* var. *pseudolepida*, and *E. micrantha* var. *micrantha*. A. Corolla limb width (mm). B. Nutlet length (mm). C. Nutlet maximum width (mm). D. Ratio of nutlet maximum width:width at apex (ca. 1/4 distance from tip). Statistical difference between a given taxon and all other taxa (via ANOVA Tukey post hoc test) indicated as: ** = $p < 0.01$. Note: box plots show median (horizontal line), first and third quartiles (boxes above and below median), and second and fourth quartiles (vertical lines); outliers indicated by small, single asterisk-like symbol (*) and extreme outliers ($> 1.5 \times$ the distance from the median to the outer quartile boundary) by small circles. Holotype measurements indicated by "t-". The placement of the two large-flowered Arizona specimens, not included in these analyses, indicated by "-a1-" (ARIZ244153) and "-a2-" (ARIZ243542).

A principal components analysis (PCA) was conducted on all samples (including the large-flowered Arizona populations) having complete data for five characters: (1) corolla limb width; (2) nutlet length; (3) nutlet maximum width; (4) nutlet width 1/4 relative distance from the apex; and (5) presence/absence of fornix bodies. A second PCA was conducted using these characters but without (5) presence/absence of fornix bodies (not illustrated). Variables were standardized by subtracting the total mean for a feature from each individual measurement, then dividing by the total standard deviation. This transformation results in all variables having a mean of zero and a standard deviation of 1. The resulting factor

scores of this PCA were plotted for the 1st versus 2nd components, 2nd versus 3rd components, and 1st versus 3rd components. The component loadings and percent of total variance explained by each axis are listed in Table 1. All statistical analyses were performed in SYSTAT, Version 11 (Systat Software, Inc., San Jose, CA, USA, <http://www.systat.com>).

Several topographic maps of all measured specimen collections were prepared, showing the distributions of specimens annotated to variety. In addition, maps were prepared of Baja California, Mexico showing more detailed representations of plant community and vegetation types.

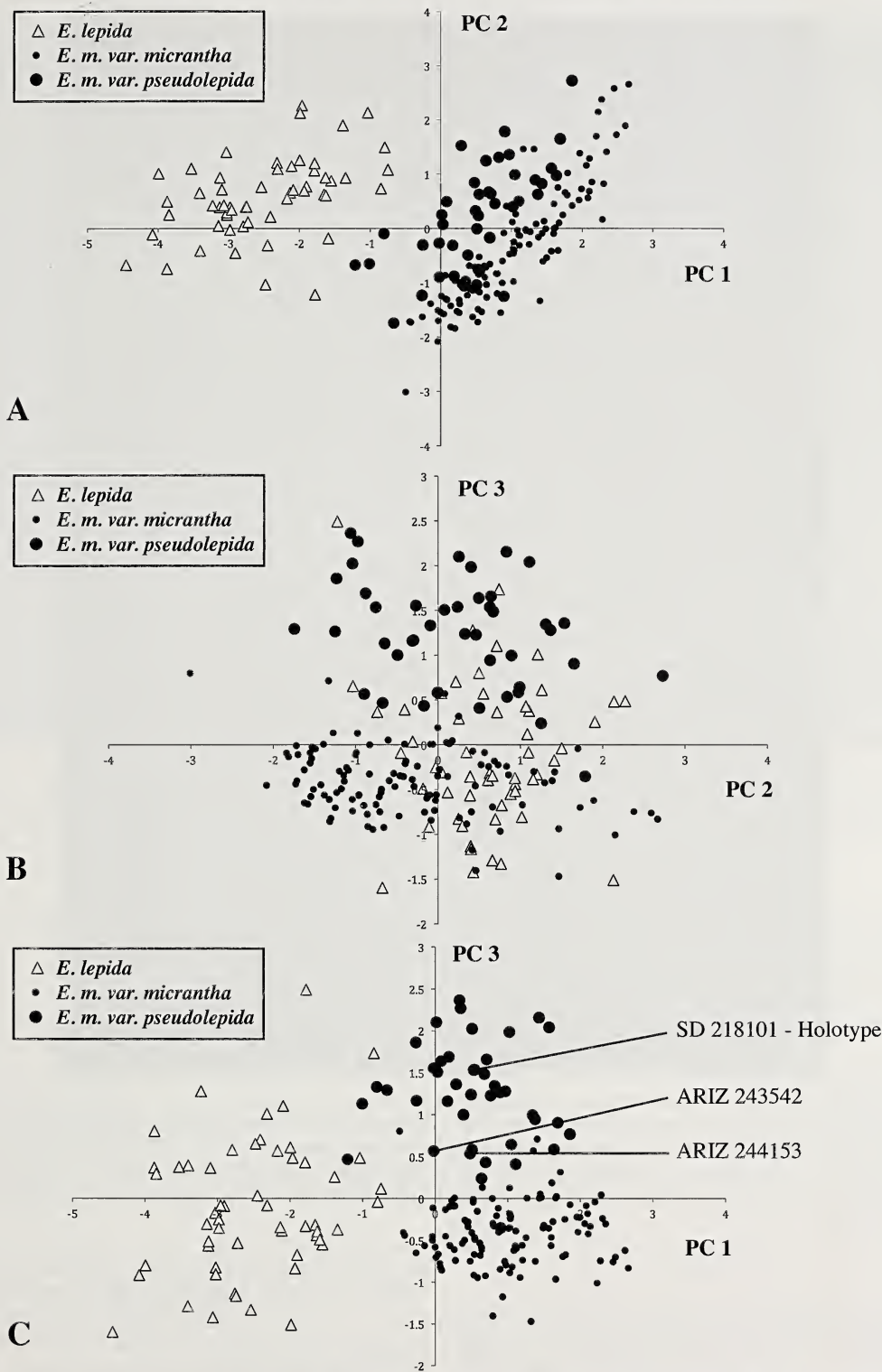


FIG. 4. Principal Components Analysis (PCA) plots. A. First (PC1) and second (PC2) factors, showing general separation of *Eremocarya lepida* from the two varieties of *E. micrantha* with overlap of the two varieties. B. Second (PC2) and third (PC3) factors, showing general separation of *E. micrantha* var. *pseudolepida* from *E. m. var. micrantha*, but overlap of *E. lepida* with both of these. C. First (PC1) and third (PC3) factors, showing general separation of all three taxa, but with some overlap. Holotype (SD218101) and two large-flowered Arizona populations (ARIZ244153, ARIZ243542) indicated by lines.

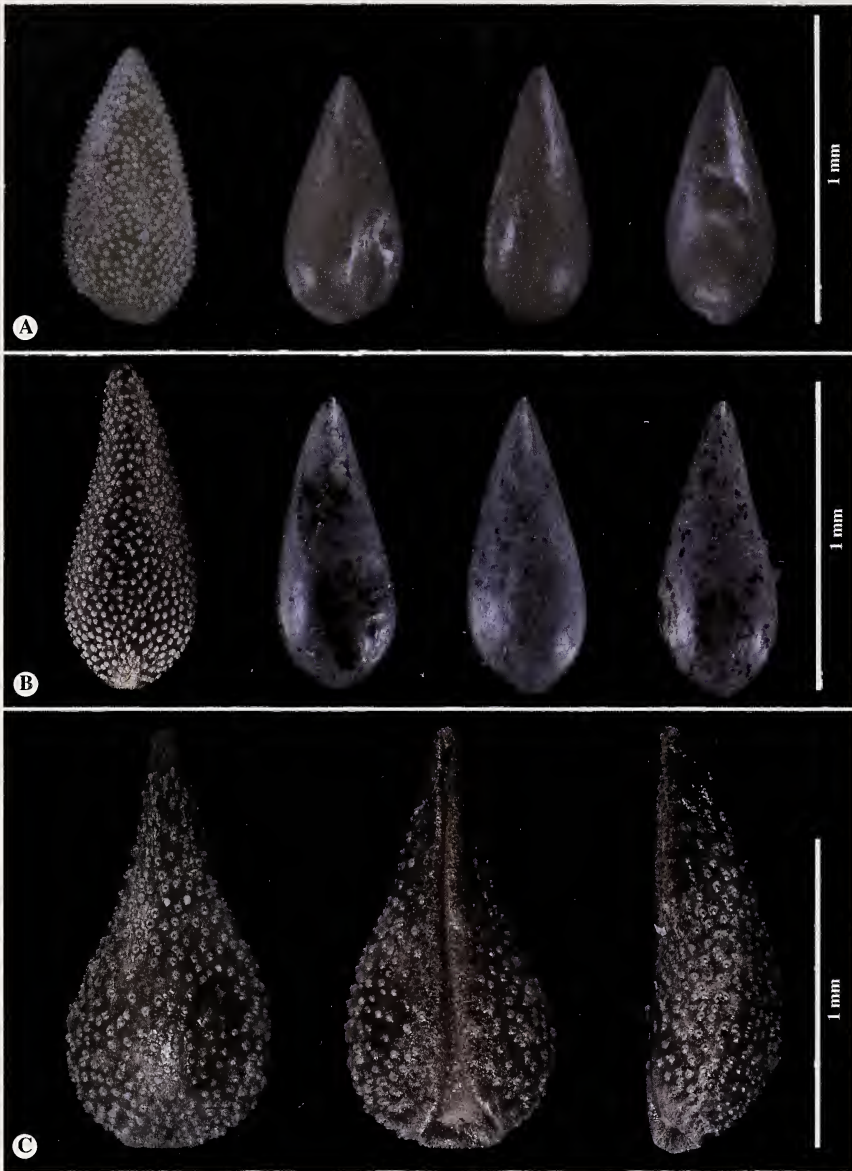


FIG. 5. Nutlet images of three taxa. A. *Eremocarya micrantha* var. *pseudolepida* (holotype: Wilder 10-116, SD218101), showing typical heteromorphic morphology with one odd, minutely tuberculate nutlet (left) and three consimilar, smooth nutlets (right). B. *Eremocarya micrantha* var. *micrantha* (Purer 4943, SD39196), showing nutlets very similar to *E. micrantha* var. *pseudolepida*, but odd nutlet slightly longer. C. *Eremocarya lepida* (Simpson 2816, SDSU17572), with homomorphic (rarely heteromorphic), larger, minutely tuberculate nutlets with an acuminate apex.

RESULTS

Field photographs of *Eremocarya micrantha* var. *pseudolepida* show most corollas having a yellow coloration at the corolla mouth (Fig. 2A, 2B, 2D). It also has floral bracts (Fig. 2B) and red-pigmented roots (Fig. 2C), which are typical of all *Eremocarya* taxa. In all specimens of *E. micrantha* var. *pseudolepida* that we examined, corolla fornicies were present, but fornix bodies were absent (Fig. 2E). Similarly,

a yellow coloration in the corolla mouth regularly occurs in *E. lepida* (Fig. 2F). In *E. micrantha* var. *micrantha*, fornicies are not evident (see Simpson et al. 2014) and the corolla mouth is generally white, occasionally obscurely yellow (Fig. 2G).

The corolla limb width of *Eremocarya micrantha* var. *pseudolepida* and of *E. lepida* are very similar (statistically indistinguishable), with both of these taxa significantly larger (with almost no overlap) from *E. micrantha* var. *micrantha* (Fig. 3A).

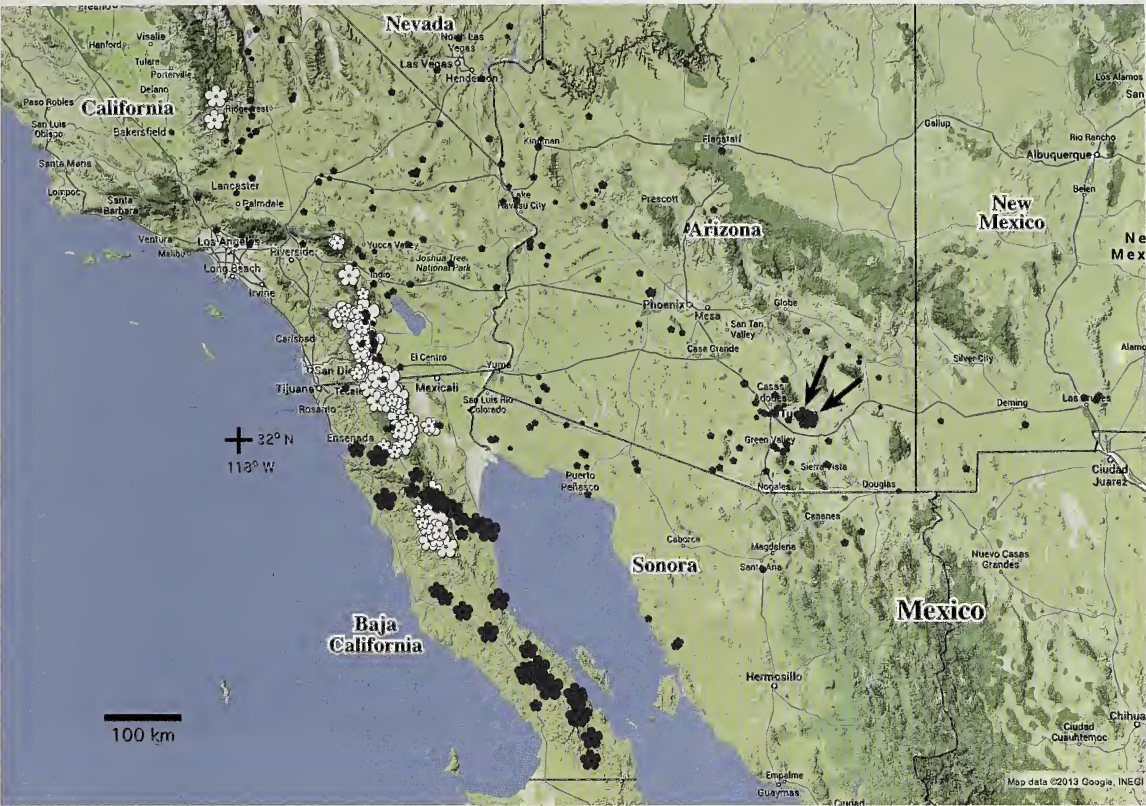


FIG. 6. Topographic map showing distribution of all measured specimens, with flower diagrams scaled to relative sizes: *Eremocarya lepida* (white flowers), *E. micrantha* var. *pseudolepida* (larger gray flowers), and *E. micrantha* var. *micrantha* (smaller gray flowers). Note two samples of *E. micrantha* var. *pseudolepida* in Arizona (arrows). Map from ©Google 2013, INEGI Data.

Nutlet lengths of all three taxa are significantly different, with *E. lepida* having larger nutlets and with *E. micrantha* var. *pseudolepida* having the smallest nutlets but the latter having considerable overlap with *E. micrantha* var. *micrantha* (Fig. 3B). Nutlet width of *E. lepida* is significantly greater than both *E. micrantha* varieties (Fig. 3C), as is the ratio of maximum nutlet width:nutlet width at 1/4 distance from the nutlet apex (Fig. 3D); for both nutlet features the two *E. micrantha* varieties are statistically indistinguishable from one another. The values for the

TABLE 1. PRINCIPAL COMPONENTS ANALYSIS LOADINGS FOR CHARACTERS USED IN ANALYSIS: Percent of total variance explained: axis 1 = 57%, axis 2 = 22%, and axis 3 = 14%.

Character	Component loadings		
	1	2	3
Corolla limb width	0.66	−0.34	−0.65
Nutlet length	0.84	0.23	0.42
Nutlet maximum width	0.94	0.15	0.10
Nutlet apical width	0.20	0.91	−0.34
Fornix body presence	0.88	−0.32	−0.06

measurements of the two large-flowered Arizona populations generally correspond to those of *E. micrantha* var. *pseudolepida*; values for the holotype specimen of *E. micrantha* var. *pseudolepida* are quite close to the mean for that taxon (Fig. 3A–D).

The PCA derived from analysis of all five characters shows some separation between all three forms of *Eremocarya*. A plot of the 1st and 2nd components shows a fairly discrete separation of *E. lepida* from the two varieties of *E. micrantha*, with some separation of the latter (Fig. 4A). A plot of the 2nd and 3rd components shows a fairly discrete separation of *E. micrantha* var. *pseudolepida* from *E. micrantha* var. *micrantha*, but with *E. lepida* overlapping both of these (Fig. 4B). A plot of the 1st and 3rd components shows discrete separation of all three taxa; in this plot the values for the two large-flowered Arizona populations largely correspond to those to *E. micrantha* var. *pseudolepida* (Fig. 4C). The first principal component, explaining 57% of the overall variance, corresponds to nutlet size (and shape when ratios are considered), with three characters (nutlet length, nutlet maximum

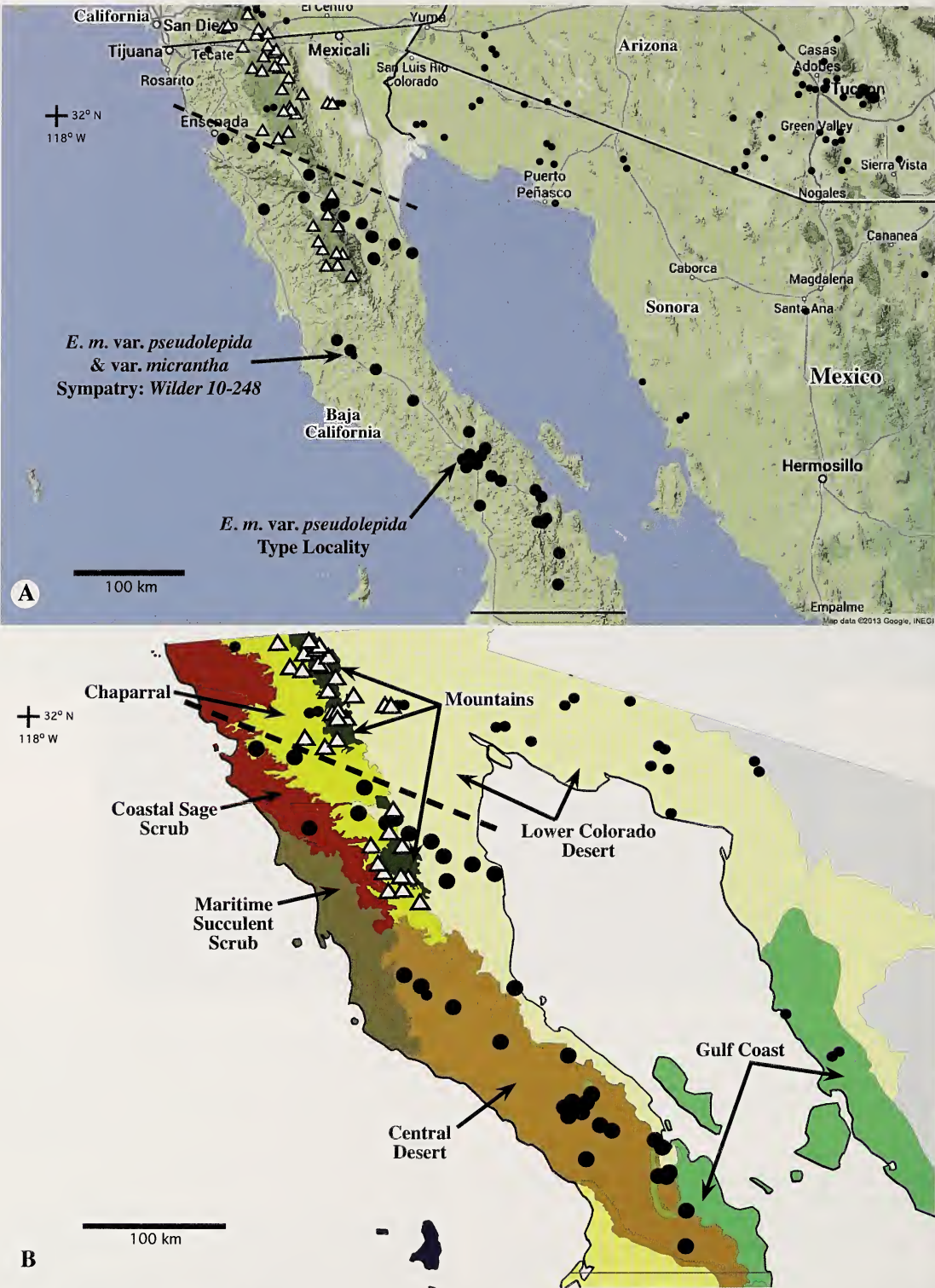


FIG. 7. Distribution maps of *Eremocarya lepida* (white triangles), *E. micrantha* var. *pseudolepida* (large black circles), and *E. micrantha* var. *micrantha* (small black circles), focusing on Baja California and mainland Mexico. A. Topographic map, showing most *E. lepida* specimens in higher elevation regions of the peninsular range and *E. micrantha* var. *pseudolepida* generally south of 32° north latitude at generally lower elevations. Arrows show locality of type specimens and of sympatric populations (from Wilder 10-248) of *E. micrantha* var. *pseudolepida* and

width, and fornix body presence) loading heavily, at 0.84–0.94 (Table 1). The second component, explaining 22% of the overall variance, corresponds to nutlet apical width, loading at 0.91. The third component, accounting for 14% of the overall variance, corresponds to corolla limb width, loading negatively at –0.65 (Table 1).

DISCUSSION

These quantitative analyses support our qualitative observations that *Eremocarya micrantha* var. *micrantha* and *E. micrantha* var. *pseudolepida* differ from one another discretely in corolla limb width, with almost no observed overlap (Fig. 3A). In contrast, *E. micrantha* var. *pseudolepida* and *Eremocarya lepida* have a very similar corolla limb width (Fig. 3A; see Fig. 2D, 2F). As cited earlier, only *Eremocarya lepida* has ever been observed to possess fornix bodies (Simpson et al. 2014); the two varieties of *Eremocarya micrantha* consistently lack them (Fig. 2E; see Simpson et al. 2014). Corolla size, measured here as limb diameter, can be difficult to measure from herbarium material; it can vary significantly within an individual, and corollas can shrink approximately 10% after being dried (see http://tchester.org/plants/analysis/cryptantha/barbigera_fergusoniae.html). However, we believe that this character, combined with others and considered with geographic range, is enough to warrant recognition of this new taxon. The general separation of the three taxa in the principal components analysis supports this conclusion (Fig. 4).

Nutlets of *Eremocarya lepida* are significantly different from both varieties of *E. micrantha* in length, maximum width, and ratio of maximum width:width 1/4 from nutlet apex (Fig. 3B–D; see Fig. 5). *Eremocarya micrantha* var. *pseudolepida* has nutlets very similar to those of *E. micrantha* var. *micrantha* (Fig. 5A, 5B), with no significant difference in nutlet maximum width or ratio of maximum width:width 1/4 from nutlet apex (Fig. 3C, 3D). However, var. *pseudolepida* does appear to have a slightly smaller nutlet length than *E. micrantha* var. *micrantha* (see Fig. 5A, 5B) although with considerable overlap between the two varieties (Fig. 3B). Our observations indicate that both varieties of *E. micrantha*

usually have heteromorphic nutlets, with one slightly larger, minutely tuberculate nutlet and three smaller, smooth nutlets (Fig. 5A, 5B). In contrast, *E. lepida* almost always has homomorphic nutlets, with all four the same size and minutely tuberculate (Fig. 5C).

A significant piece of evidence for our recognition of this new taxon comes from geographic range data (Figs. 6–8). Variety *pseudolepida* is found only (or largely; see below reference to Arizona populations) in Baja California, Mexico, a little below 32° north latitude (Fig. 6–8). Most populations of var. *pseudolepida* occur in the Central Desert region of the Sonoran Desert, but several are found in the southern Lower Colorado Desert region, as well as in the southern regions of both the Chaparral and Coastal Sage Scrub regions of the California Floristic Province (Fig. 7B). We struggled with the appropriate rank for this new taxon but chose the rank of variety to be consistent with past treatments for other members of this taxonomic complex. For example, in the closely related genus *Cryptantha*, *C. barbigera* var. *barbigera* (A. Gray) Greene and *C. barbigera* var. *fergusonae* J.F. Macbride are virtually identical except for a small versus large corolla limb width (see Kelley et al. 2012). Given that the two *E. micrantha* forms are very similar in nutlet morphology and that both lack the fornix bodies of *E. lepida*, we think that varietal status is appropriate at this time. However, we reiterate that *E. micrantha* var. *pseudolepida* has an almost separate geographic range, whereas the ranges of *E. m.* var. *micrantha* and *E. lepida* partially overlap (although generally separated by elevation).

From our study of herbarium specimens, we discovered two unusual Arizona specimens of *Eremocarya*: *Bowers R34*, 18 Apr 1982, ARIZ244153 and *Bowers R1152*, 1 May 1983, ARIZ243542. Both of these specimens have a nutlet morphology and absence of fornix bodies similar to *E. micrantha* (Fig. 3B–D), but they have a large corolla size that fits the range of *E. micrantha* var. *pseudolepida* (Fig. 3A; see Fig. 4C). These large-flowered specimens (reportedly located very near one another) are restricted to the east side of the Mica Mountain/Rincon Peak region just east of Tucson in southeastern Arizona (Fig. 6). Although the corolla morphology of these fits our circumscription of

←
E. m. var. *micrantha*. Map from ©Google 2013, INEGI Data. B. Vegetation map, showing (1) *E. lepida* largely restricted to the mountains of the peninsular range; (2) *E. micrantha* var. *pseudolepida* occurring in the Central Desert and Lower Colorado Desert regions, with some populations in coastal sage scrub and chaparral regions; and (3) *E. micrantha* var. *micrantha* occurring in the Lower Colorado Desert of Baja California and adjacent Sonora, Mexico, with some populations in the northern Chaparral region of Baja California and Gulf Coast region of mainland Mexico and one sympatric population in the Central Desert of Baja California. Dashed line in both maps indicates boundary separating almost all specimens of the two varieties of *E. micrantha* in Baja California.

E. micrantha var. *pseudolepida*, their highly disjunct distribution from the Baja California concentration of var. *pseudolepida* is puzzling. An examination of these two Arizona collections indicates some possible differences in leaf shape and calyx vestiture; however, we caution that these features largely fall into the range of features of the Baja California specimens and may simply represent local phenotypic variation. We hesitate at this time to list these two Arizona collections as paratypes of our new variety described here. The fact that the label of one of the two collections (*Bowers R34*) records the habitat as “moist soil near streambed in riparian woodland” may lead credence to the possibility that the local environment influenced an atypical floral morphology, as members of *Eremocarya* are not generally found in a habitat with appreciable long-term moisture as implied here. In addition, during the years of collection (1982 and 1983), the area was heavily impacted by cows, both in terms of grazing and manure deposition (George Ferguson, University of Arizona Herbarium, personal communication, April 2015), these altered conditions possibly influencing a phenotypic shift in corolla size. The other possibility is that these are indeed members of our new variety and that these populations arrived from the main Baja California populations by long distance dispersal (perhaps via bird migration, this possibly supported given the riparian habitat as a potential resource for a bird stop-over of at least one Rincon Mountain population) or that they are vestiges of an ancestral vicariant event.

Phylogenetic analyses using molecular data are needed to resolve whether these Arizona populations are part of the Baja California var. *pseudolepida* complex or represent a case of convergent evolution. Such a study, involving extensive sampling of all three taxa, is planned for the near future. However, the large-flowered Arizona herbarium specimens are too old to extract good quality DNA or grow plants from seed. A rigorous attempt in April 2015 to relocate these Arizona populations was unsuccessful, but we will keep trying. Until that is done, the status and relationships of these large-flowered Arizona populations may remain a mystery.

The three taxa of *Eremocarya* have significantly different elevations (boxplot not shown), although with considerable overlap. *Eremocarya lepida* has the highest average elevation, at 1,315 m (200–2,200 m, SD ± 436 m). This correlates well with our knowledge of these taxa, with *E. lepida* found at higher elevation in mountainous and desert transition regions of the Peninsular Range (Simpson et al. 2014) (Fig. 6, 7). The average elevation of *E. micrantha* var. *micrantha* is 759 m (9–2,131 m, SD ± 492 m). That of *E.*

micrantha var. *pseudolepida* (not including the two Arizona populations) is lowest at 510 m (range 10–1,250 m, SD ± 303 m). Thus, even though the ranges of *E. lepida* and *E. micrantha* var. *pseudolepida* interdigitate to some degree (Fig. 6–8), they would not be expected to be sympatric, given these differences in elevation and vegetation regions. The two disjunct Arizona populations have elevations higher than any *E. micrantha* var. *pseudolepida* populations in Baja California, the former at 1,560 m (ARIZ243542) and 1,310 m (ARIZ244153). Although not considerably higher than the highest Baja California collection of var. *pseudolepida* (1,250 m), the relatively high elevation of these large-flowered Arizona populations underscores their aberrant nature.

Aside from the anomalous Arizona populations, *Eremocarya micrantha* var. *pseudolepida* is almost entirely allopatric from *E. micrantha* var. *micrantha*, the latter occurring north of about 32° latitude on the Baja peninsula, although there are a few small populations much further south in Sonora on the Mexican mainland (Figs. 6, 7). The one exception we discovered is a single collection in the middle of the range of *E. micrantha* var. *pseudolepida* (*Wilder 10-248*, ARIZ408961, SD218100, UCR; locality indicated in Fig. 7A), two sheets of which (ARIZ and UCR) contain a mixture of both varieties of *E. micrantha* (personal observation of UCR specimen by Andy Sanders). Interestingly, we saw no evidence of introgression between the two varieties in this limited sampling. The fact that they can grow together in at least one population without apparent interbreeding may be supportive of their having genetic differences. However, nothing is known of the breeding system in this genus. We are hypothesizing that *E. m.* var. *pseudolepida* is outcrossing, given its relatively large corolla size. *Eremocarya m.* var. *micrantha* may well be selfing, given its very small corolla size. But, this is all speculation in the absence of observational or experimental studies of reproductive biology.

One interesting facet of the biogeography of *Eremocarya micrantha* var. *pseudolepida* is its distribution across what we term the “Baja California Trans-Peninsular gap,” a lower elevation zone between the Sierra de San Pedro Martir and the Sierra de Juarez (Fig. 8). In this area a mapped desert “arm” extends westward from the Colorado Desert well into the more Mediterranean region of the California Floristic Province, potentially enabling desert-adapted species to disperse from east to west into these lower elevation cismontane habitats without traversing the high elevation mountains. Additional species typical of the Colorado/Sonoran Desert that occur both in the Baja California Trans-Peninsular gap and in pockets of more arid microhabitats

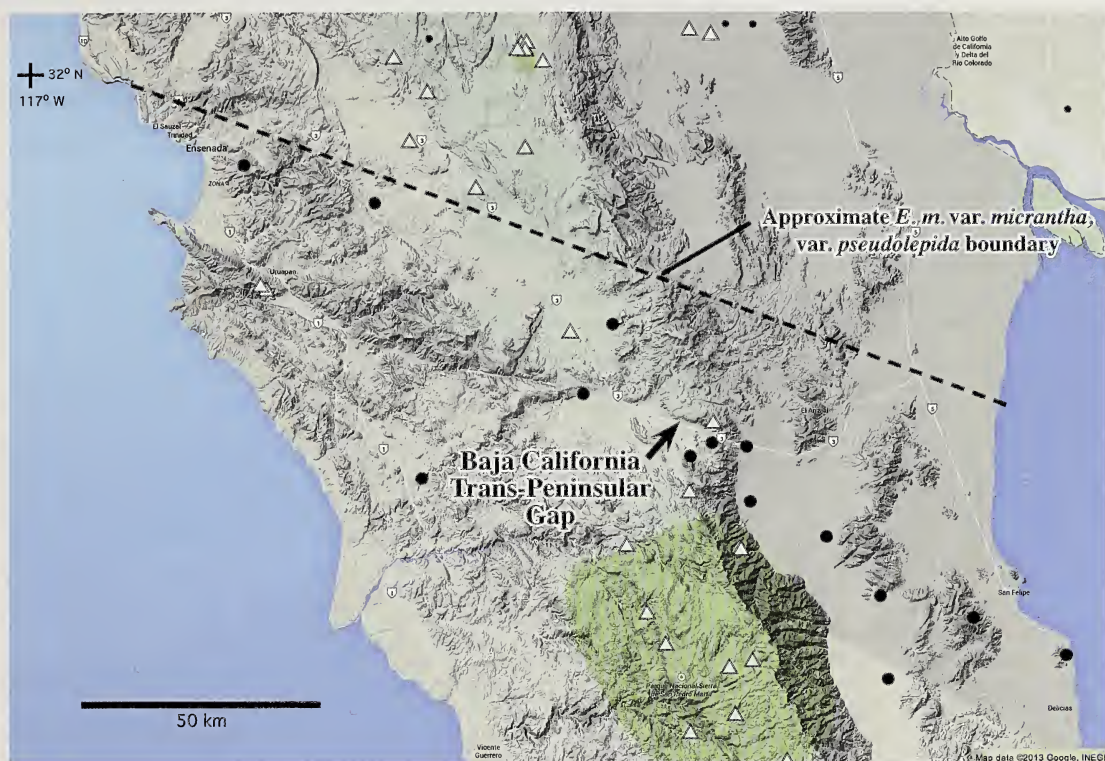


FIG. 8. Topographic map of *Eremocarya lepida* (white triangles), *E. micrantha* var. *pseudolepida* (large black circles), and *E. micrantha* var. *micrantha* (small black circles), focusing on northern Baja California. Note boundary (dashed line) separating almost all specimens of the two varieties of *E. micrantha* in Baja California. Arrow shows location of Baja California Trans-Peninsular Gap, a possible dispersal corridor across the peninsular range. Map data from ©Google 2013, INEGI Data.

in northwestern Baja California include *Palafoxia arida* B.L. Turner & M.I. Morris var. *arida* (Asteraceae), *Enneapogon desvauxii* P. Beauv. (Poaceae), *Eriogonum fasciculatum* Benth. var. *flavoviride* Munz & I.M. Johnst. (Polygonaceae), *Nicotiana obtusifolia* M. Martens & Galeotti (Solanaceae), and *Boerhavia coccinea* Mill. (Nyctaginaceae). Although we cannot know definitively without perhaps detailed molecular studies, we hypothesize that the direction of dispersal of our new taxon occurred from east to west across this gap, allowing for the movement of this desert-adapted taxon into arid microhabitats of chaparral and coastal sage scrub.

Future molecular studies will be needed to evaluate the evolutionary history of *Eremocarya* entities with respect to their taxonomic status and character state changes. These studies will, we hope, help to assess the taxonomic rank of the three entities as recognized here, perhaps based on branch lengths and assessment of reciprocal monophyly. Current phylogenetic analyses (Hansenstab-Lehman and Simpson 2012) indicate that *Eremocarya* is the sister taxon to the genus *Oreocarya* Greene, whose members are high elevation perennials, many with relatively large flowers. If this relationship continues to be

supported, a fascinating question will be the morphology of the common ancestor of these two genera. This may help to answer the ancestral corolla size in *Eremocarya* and what possible selective pressures might have influenced a subsequent shift in size. How has habitat, particularly as related to elevation, influenced this evolutionary shift? How does this relate to reproductive biology and possible pollinator shifts? We presume that the distinctive fornix bodies of *E. lepida* are derived; work is underway to elucidate their possible function.

Chromosome counts of both *Eremocarya lepida* (*Cryptantha micrantha* subsp. *lepida* in their paper) and *E. micrantha* var. *micrantha* (*C. m.* subsp. *micrantha* in their paper) were done by Mathew and Raven (1962), who determined a count of $n = 12$ for both taxa. There are no known chromosome counts for *E. micrantha* var. *pseudolepida*, so possible polyploidy or aneuploidy in the latter cannot be assessed at this time. We hope to obtain a count of *E. micrantha* var. *pseudolepida* in the near future. Finally, as pointed out, nothing is known of the breeding system of members of this genus. We hope to at least determine if the three entities are capable of selfing or outcrossing.

KEY TO THE TAXA OF *EREMOCARYA*

The following revised key to the two species of *Eremocarya* including infraspecies (modified from Simpson et al. 2014, Kelley and Simpson in prep.) may be used to more effectively identify them.

- 1. Corolla limb 0.5–1.5 mm diam., center white, rarely obscurely yellow *E. micrantha* var. *micrantha*
- 1. Corolla limb 1.5–4.8 mm diam., center generally prominently yellow, rarely white
 - 2. Nutlets usually homomorphic, minutely tuberculate, 1.2–1.4 mm long, apex acuminate; corolla fornice each with a basal cluster of tiny (ca. 0.1 mm long), pendant, ellipsoid “fornix bodies;” southern California to northern Baja California, Mexico *E. lepida*
 - 2. Nutlets usually heteromorphic, with one slightly larger, minutely tuberculate nutlet and three smaller, smooth nutlets, the largest ca. 1–1.1 mm long, apex narrowly acute; corollas lacking “fornix bodies;” mostly from Baja California south of 32° north latitude *E. micrantha* var. *pseudolepida*

Note in proof: We have recently become aware of a specimen (*Schmidt 2649*, 18 April 1998, MO04884946) that appears quite similar to the two large-flowered Arizona specimens (ARIZ244153 and ARIZ243542) examined in our study, having a corolla limb diameter of 2.5–3.4 mm (measured from an herbarium sheet scan). This MO specimen has a locality (32° 08' 14" N, 110° 28' 52" W, 1250–1380 m. elev., all information indicated on the label) approximately 1.7 mi (2.7 km) south-southeast of the two ARIZ specimens. It may provide sufficiently recent material for future DNA studies. We plan to search for this population in future field work.

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APPENDIX 1

VOUCHER SPECIMENS OF *EREMOCARYA* USED IN THIS STUDY (MINUS THE *E. MICRANTHA* VAR. *PSEUDOLEPIDA* TYPES AND LARGE-FLOWERED ARIZONA SPECIMENS CITED EARLIER), LISTED ALPHANUMERICALLY BY COLLECTOR AND COLLECTION NUMBER; DATE LISTED FOR COLLECTIONS WITHOUT A COLLECTION NUMBER (S.N.). ALL SPECIMENS WERE VERIFIED AND MEASURED IN ONE OF BOTH OF THE QUANTITATIVE STUDIES.

Eremocarya lepida: Abrams 2904 (UC407303); Alameda 6544 (CAS831263); Anderson 26 (SDSU10277); Bourell 2980 (CAS741818); 9 June 1951, Brattstrom s.n. (SD44489); Breisch 270 (SD194947); Breisch 449 (SD201471); Clemons 1289 (SD118945); Copp 14 (CAS840487, SD134020); 1 May 1933, Cota s.n. (SD15615); Eastwood 9422 (CAS26923); Eastwood 9539 (CAS26924); Gander 5123 (SDSU5412); 10 June 1933, Gander s.n. (SD4195); 11 June 1933, Gander s.n. (SD4194); Grimmell 282 (CAS26926); Hendrickson 1953 (SD196338); 17 June 1971, Howell s.n. (CAS862225); 18 June 1922, Jaeger s.n. (DH140398); Levin 1674 (SD119269); Macias 463 (BCMEX011181, SD165072); Marsden 491 (SD205615); Marsden 578 (SD205614); McGill 8726 (DES00004221); Moran 3430 (SD48056); Moran 10923 (SD53840); Moran 11126 (SD54693); Moran 13869 (SD64660); Moran 13898 (SD64661); Moran 14381 (SD79677); Moran 14475 (SD79678); Moran 14906 (SD72336, UC1361697); Moran 15001 (SD69225); Moran 21288 (SD86898); Moran 22039 (SD91906); Moran 22063 (SD91864); Moran 22143 (SD91487); Moran 23334 (SD96974); Moran 24086 (SD971110); Moran 27342 (SD103646); Moran 27427 (SD103440); Moran 27448 (SD103457); Moran 28894 (DES00024907, SD105525); Moran 30665 (SD111068); Nenow 1103 (SD221038); Otis 7 (SD201473); Rebman 7210 (SD155824); Rebman 17601 (SD197223); Rebman 21146 (SD213030); Reeder 7193 (ARIZ216244); 17 June 1971, Roos s.n. (CAS905666); Ross 2598 (UC 1584224); Shevock 1074 (CAS713389); Simpson 2369 (SD180702); Simpson 2369 (SDSU17281); Simpson 2816 (SDSU17572); Simpson 3109 (SDSU18628); Simpson 3184 (SDSU19533); Simpson 3320 (SDSU19612); Simpson 6VI91AB (SDSU5418); Simpson 6VI91AC (SDSU5388); Suttikus 73-23-14 (DES00065387); Sweet 266 (SD178709); Thorne 55789 (SD124127); Thorne 55937 (SD124128); Thorne 60451 (SD124983); Thorne 61669 (SD124981); 29 May 1983, Thorne s.n. (BCMEX001288); 15 March 2003, Vinton s.n. (SD182665); 16 May 2003, Vinton s.n. (SD182666); Wedberg 909 (SDSU5046); Wiggins 9808 (UC718873); Wiggins 11809 (SD47301); Wolf 8019 (ARIZ142056); Wolfinger 133 (SD217612).

Eremocarya micrantha var. *micrantha*: Howe 2625 (SDSU5400); Barth 407 (SD169356); Beatley 3715 (DH595377); Beauchamp 2192 (SD85416); Benson 9972 (ARIZ13871); Benson 10029 (ARIZ13870); Bowers 3127 (ARIZ259823); Burgeas 6850 (ARIZ259530); Butterwick 4513 (DES00020253); Butterwick 6442 (ARIZ228881); Christian 819 (ARIZ161721); Clemons

1634 (SD120961); Clemons 2020 (SD122612); Clokey 5926 (CAS380904); Clokey 8731 (ARIZ417391, CAS380903); Cronquist 10192 (DH592832); Crooks 7081 (ARIZ417366); 19 April 1938, Crooks s.n. (ARIZ417367); Devender 934 (ARIZ235363); Devender 91-19 (ARIZ291266); Douglas 933 (DES00045237); 17 April 1931, Eastwood s.n. (CAS190280); Eggleston 19869 (ARIZ38372); Engard 445 (DES00011367); Felger 1973 (ARIZ189161); Felger 7552 (ARIZ365678); Felger 17377 (SD96180); Felger 17801 (ARIZ200634); Felger 19026 (ARIZ188812); Felger 19571 (ARIZ368315); Felger 20363 (ARIZ189177); Felger 20793 (ARIZ189187); Felger 92-163A (ARIZ300111); Felger 93-252 (ARIZ303542); Felger 93-388 (ARIZ342450); Felger 96-164 (ARIZ371716); Fischer 6039 (ARIZ350332); Fishbein 10 (ARIZ300476); Fishbein 2013 (ARIZ315946); Fishbein 2256 (ARIZ319065); 29 April 1967, Forister s.n. (DES00006733); Gallup 193 (SDSU5425); Gander 134 (SD10507); Gentry 49 (ARIZ274030); Gooding 21-54 (ARIZ120707); Gould 3055 (ARIZ20751); Gould 3672 (ARIZ73131); Gregory 667 (SD158771); Groot 6587 (SD219000); Guertin 448 (ARIZ366079); Williams 602 (SDSU18956); Hammond 11795 (ARIZ379156); Harrison 7719 (CAS193407); Hendrickson 2640 (SD203297); Hendrickson 2784 (SD205617); Hendrickson 4588 (SD210829); Hevron 1622 (ARIZ304531); Higgins 13050 (DES00028221); Hodgson 3508 (DES00029290); Hodgson 5673 (DES00034517); Hodgson 7087 (DES00037500); Hodgson 16928 (DES00052687); Hodgson 17188 (DES00053987); Hodgson 17584 (DES00003630); Hodgson 17604 (DES000061111); Hodgson 21821 (DES000065422); Hodgson 24816 (DES000067821); Hodgson 28450 (DES000068009); Holland 1025 (DES00042570); Hoover 753 (DES00030752); Howe 2903 (SDSU5419); Jenkins 91-9 (ARIZ291265); May 21, 1884, Jones s.n. (ARIZ417393); Jordan 99 (ARIZ201923); Leon 3465 (ARIZ417780); Licher 2293 (DES00070122); Marsden 538 (SD205618); Mason 1810 (ARIZ143493); Mason 2555 (ARIZ159388); Mason 3114 (ARIZ199882); McGill 6405B (DES00003630); McLaughlin 3152 (ARIZ261818); McLaughlin 4366 (ARIZ305675); McLaughlin 9133 (ARIZ372369); Moran 30772 (SD111259); Morefield 3262 (ARIZ282195); Morefield 3596 (ARIZ284151); Morgan K83 (SDSU5421); Parker 7427 (ARIZ85736); Peebles 6975 (CAS252113); Phillips III-1973 (ARIZ187426); Purer 4943 (SD39196); Rea 657 (ARIZ262507); Rebman 21541A (SD213031); Rickard 1853 (DH562256); 10 March 1940, Rose s.n. (CAS275467); Salywon 1050 (DES00059734, SD188428); 13 March 1982, Scheidlinger s.n. (SDSU18155); Shreve 6217 (ARIZ98294); Shreve 6217 (ARIZ98294); Shreve 7891 (ARIZ98293); Simpson 3126 (SDSU19604); Simpson 3670 (SDSU20043); Simpson 5IV97C (SDSU12434); Smith 998 (ARIZ216616); 21 March 1906, Spalding s.n. (ARIZ98295); Sweet 509 (SD200747); Tedford 630 (ARIZ388080); Thornber 2171 (ARIZ417362); Thornber 2473 (ARIZ417392); Thornber 4632 (ARIZ417370); Thornber 4711 (ARIZ417364); Thornber 4892 (ARIZ417361); Thornber 5300 (ARIZ417396); Thornber 5780 (ARIZ417394); April, 1908, Thornber s.n. (ARIZ417369); 19 April 1913, Thornber s.n. (ARIZ417373); 12 April 1903, Thornber s.n. (ARIZ417363); 12 May 1905, Thornber s.n. (ARIZ417368); Tiehm 10504 (DES00031364); Tiehm 11084 (DES00032535); Tiehm 16118 (DES00067729);

Turner 68-94 (ARIZ169031, SD78609); White 2721 (SDSU5394); 19 April 1905, Wooton s.n. (DH137011, DES00016498); Whitehead 404 (DES00014812); Wiggins 8408 (ARIZ20120); Wiggins 14053 (ARIZ144634); Wiggins 21595 (ARIZ187144); Wojtan 4IV92C (SD67704); Worthington 24333 (DES00039956); Worthington 24534 (DES00039908); Yatskievych 85-20 (ARIZ259773).

REVIEW



The tanoak tree: an environmental history of a Pacific Coast hardwood. By FREDERICA BOWCUTT. University of Washington Press, Seattle, WA. 240 pp. ISBN 97802959 94642. Price \$35.00 (hardcover, paperback not available).

In a time of biodiversity crisis, detailed cultural, ecological, and economic studies of at risk species are of great value. In a timely and compelling single volume Frederica Bowcutt presents a thorough presentation of *Notholithocarpus densiflorus* (Hook. & Arn.) P. S. Manos, C. H. Cannon & S.H. Oh, the familiar tanoak tree to residents and enthusiasts of coastal California, coastal southwestern Oregon, and northern Sierra Nevada foothill forests. The book brings to light the changing perspective on this species over the last one hundred and fifty years by post-settlement economies. This is done in the context of the unchanging reverence and value placed on tanoak by California and Oregon Indians. The utility and value of tanoak products is broadly recognized by native peoples, yet the perspective of western commodity-driven forest economies have shifted from valuing tanoak products to a pervasive view that this common tree is the central impediment to production of Douglas fir and redwood. Bowcutt describes how these shifts placed great pressure on tanoak beginning with widespread and unsustainable bark harvesting and continuing to widespread use of herbicides to reduce competition with conifers. A century ago Willis Linn Jepson recognized tanoak as undervalued ecologically and yet overexploited by a tanning industry which relied on tanoak-bark derived tannins prior to the advent of chemical alternatives (Jepson 1911). His concern for the species resonates today but in a way incongruous to his initial concern. Currently, tanoak is at risk from a low perceived value among foresters and the devastating emergent pathogen *Phytophthora ramorum* Werres, de Cock & Man in't Veld, the cause of sudden oak death. By presenting a

detailed analysis of historical and contemporary tanoak products Bowcutt challenges the widespread belief that this tree has little economic potential. By taking this approach, the book illuminates the ongoing loss of cultural and ecological resources wrapped up in tanoak and leaves the reader informed on current issues threatening this widespread and common tree.

Bowcutt's book will be of interest to specialists and non-specialists alike as it is well written and researched. It achieves a quality greatly valued by the reader: it can be read casually and serves as a guide to a diverse literature. "The Tanoak Tree" will inevitably draw comparisons to Susan Freinkel's "American Chestnut" (Freinkel 2007) in that both books present a historical account of culturally and economically important trees which have been devastated by invasive pathogens. An important contrast between the two books is that the story of American Chestnut is retrospective while the threats to tanoak and its regional decline are happening in the present. Management decisions that will affect the spread and impacts of sudden oak death are increasingly directed at Humboldt and Del Norte counties where the disease threatens many individual tanoak trees and groves which are actively used and managed by regional native peoples; these events make the book especially timely. In addition to acting as an excellent natural history guide to tanoak, this book is a must-read for researchers and practitioners of tanoak issues as well as those who work on regional tree declines outside of the western US. The book also serves as a point of departure for individuals seeking an informed perspective on the threats to tanoak - information critical to engaging in the ongoing discussion and actions aimed at the conservation of this important tree.

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REVIEW



Field Guide to Manzanitas
California, North America, and Mexico

Michael Kauffmann, Tom Parker, and Michael Vasey
Photographs by Jeff Bisbee

Field guide to manzanitas: California, North America, and Mexico. By M. E. KAUFFMANN, V. T. PARKER, M. C. VASEY, WITH PHOTOGRAPHS AND J. BISBEE. Backcountry Press, Kneeland, CA, in association with California Native Plant Society, North Coast Chapter. 170 pp. ISBN 978-1-941624-02-9. Price \$27.95 (paperback).

The Field Guide to Manzanitas by Kauffmann et al. ushers in a refreshing approach to botanical field guides. Like the nascent inflorescences of manzanitas bursting into flower after their long wait, the field guide is a bundle of knowledge that electrifies the reader and inspires the user. It was conceived, designed, and written in such a way to guarantee you will fall in love with manzanitas and become knowledgeable about their biogeography and identification. It is a field botanist's dream!

The field guide is so thoughtfully and carefully formatted that your enjoyment and increased wisdom is certain. The main section of the guide is titled Manzanita Treatments where all 105 taxa in the genus *Arctostaphylos* are discussed in alphabetical order to make quick reference and rapid assessment easy. Each species is given one page (Species Plate) with more pages allocated to subspecies. Everything you need to identify your specimen is right there on the page including the essential range maps. Each species is illustrated with three or four defining images with clear and precisely worded captions so that you see exactly what you need for identification.

This allows character comparisons of all manzanita species. Using comparable characters in keys and field treatments is an excellent means to convey identifiable traits that may be necessary to separate species and are especially important in manzanitas where many species often grow together. A few brief descriptive words are used after each character type. While manzanita identification isn't rocket science, this consistent approach enabling us to tease out the character differences is superb.

The Manzanita Characters section includes vivid illustrations, photographs, and explanations to illuminate the important variation on key characteristics like stems, burls, leaves, fruits and inflorescences. Throughout the book, you become

enlightened with exquisite photographic images of bark and burls, colorful flowers and fruits, bracts and hairs. Hairs with or without glands and images of leaves carefully show their shape and basal outline, while highlighting whether they are auriculate (heart-shaped) or truncate, for example. The images and character descriptions are displayed in a consistent and comparative style that allows you to readily differentiate one species from another. These are presented with habitat and plant community associations, gorgeous landscape imagery, detailed range maps, and more.

There are other marvelous features in the Field Guide to Manzanitas that fulfill a field botanist's dream. The authors state that their purpose in this field guide is to "lift the veil" on this quintessentially California shrub. Ecology and evolution is thoughtfully addressed. *Arctostaphylos* evolved with the California Floristic Province with unusually high local endemism driven by harsh conditions, poor, low nutrient soils, and the eventuality of fire. The story of diversification began some 110 million years ago during the late Cretaceous with the emergence of the Ericaceae and subsequent lineages springing forth. The ecology section describes the influence of fire and smoke, the importance of mycorrhizal fungi, and describes dispersal where rodents are the key agents. Just before the Manzanita Treatments another field botanist dream is realized through Regional Keys focusing on the California Floristic Province, divided into the Klamath Mountains, the San Francisco Bay, the Central Coast, the Sierra Nevada, the Southern California, the Baja California, and Outside of the California Floristic Province.

The Field Guide to Manzanitas is an essential contribution to California botany and field guides. The story of the authors coming together is filled with interesting chance events and meetings that led to the making of the guide. It was during one of these chance events that the photographer, Jeff Bisbee, put his tracking sights and photographic talents to the genus *Arctostaphylos*. Before manzanitas, Jeff worked many years tracking and photographing conifers throughout Mexico and elsewhere in Western North America. On one occasion when Jeff was speaking on Mexican conifers at UC Santa Cruz he decided to visit the Santa Cruz Cypress population on Butano Ridge. He asked for local help to gain shorter access through locked gates and it was on this occasion that he met Mike Vasey. Mike and Jeff drove together to the trailhead and during their short two-hour drive a new manzanita-tracking project was born. Over

the next three years Jeff travelled and photographed every species and subspecies of *Arctostaphylos* in every phenological stage in order to capture flowering, fruiting, onset of nascent inflorescences, and in many instances recovery after fire.

It was also during this time that Michael Kauffman was finishing the guide maps for his book, *Conifer Country* (2012) and clearly his interests in conifer tracking were closely allied with Jeff's, so naturally the two began a great friendship.

It's easy to imagine the rest of the Field Guide coming together once there was a clear *Arctostaphylos* map and field identification enterprise in

motion. Tom Parker and Mike Vasey put their deep knowledge and vast experience with *Arctostaphylos* to the task and before many California botanists knew there was a Manzanita Field Guide in the making... it was finished!

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